

Chapter 1. Introduction

1.1. Cambrian Chronostratigraphy

For over 100 years the traditional Cambrian period was subdivided into the Lower, Middle and Upper Cambrian based on the original concepts of Walcott (1889; 1890a, b) and Brøgger (1878, 1882, 1886). The three divisions were of different lengths of time and presented major problems for global correlation (Robison *et al.*, 1977; Fletcher, 2003; Geyer, 2005 in Peng *et al.*, 2013). The presence of a prolonged lower Cambrian (Landing, 1994, 1998; Geyer and Shergold, 2000), approximately equivalent in length of time to the traditional Middle Cambrian and Upper Cambrian combined, led to a mission by the ICS to subdivide the Cambrian system into four parts of similar lengths of time (Landing, 1994; Palmer, 1998; Geyer and Shergold, 2000; Peng *et al.*, 2004b; Babcock *et al.*, 2005). The traditional Lower Cambrian was to be divided into a pre-trilobitic series and a trilobite-bearing series each to be divided into two stages. The third and fourth Cambrian series were to be based largely on the traditional Middle and Upper Cambrian, with each of these series subdivided into three stages. This proposal was ratified in 2004 by the International Subcommittee of the Cambrian System (ICS). The main objective of the ICS is the development of an internationally applicable global chronostratigraphic scheme for the Cambrian System which can be used for stratigraphic correlation (Alvaro *et al.*, 2013). The boundary positions or Global Standard Stratotype-section and Points (GSSPs) between these stages correspond to recognizable intercontinental horizons. To date, two Cambrian series remain to be defined – the provisionally named Series 2 and Series 3. The greater faunal diversity in the upper half of the Cambrian allowed the subdivision of Series 3 into three stages, with definitions based on the first appearance datum (FAD) horizons of key agnostid species (see Fig.1-1). Due to the lack of uniformity between regional stage 25 definitions in the past, various names exist for

the regional stages. Sometimes the terminology even varies within individual regions (Babcock *et al.*, 2011).

Extensive stratigraphic studies have been conducted throughout the world since these decisions were made in order to resolve correlation problems in the various Cambrian biogeographic realms and provinces and to establish Global boundary Stratotype Sections and Points (GSSPs). The present study of Cambrian Series 3 trilobites and agnostids from Australia adds considerable data that will refine the Cambrian chronostratigraphic chart and aid in global correlation.

Series	Stage	GSSPs
Furongian	Stage 10	FAD of <i>Lejopyge laevigata</i> FAD of <i>Acidusus atavus</i> FAD of <i>Oryctocephalus indicus</i> / <i>Ovatoryctocara granulata</i>
	Jiangshanian	
	Paibian	
Series 3	Guzhangian	
	Drumian	
	Stage 5	
Series 2	Stage 4	
	Stage 3	

Figure 1-1. Stages of Cambrian Series 3 and the taxa that define their ratified (Drumian and Guzhangian) or proposed (Stage 5) GSSPs based on the First Appearance Datum (FAD) concept (adapted from Fig. 19.2, Peng *et al.*, 2012).

1.1.1. Cambrian Series 3

Cambrian Series 3 spans a period of time from ~509 to 497 Ma (Peng *et al.*, 2012). The period does not strictly equate to the traditional Middle Cambrian but is expanded in concept and represents a time when trilobites recovered from a mass extinction event near the end

of Series 2 (Alvaro *et al.*, 2013). Traditionally, trilobites and agnostids have been the most effective tool for large-scale chronostratigraphic and palaeobiogeographic analyses during most of the Cambrian period, especially during the latter half when they showed remarkable diversification after their biomineralisation during Cambrian Series 2 (Peng *et al.*, 2012; Hally and Paterson, 2014). However, trilobites and agnostids show differing biogeographic distributions and hence have different correlation value. Trilobites tend to be endemic to certain regions or palaeocontinents and are of best use for correlating continental shelf and platform deposits (Robison, 1976; Babcock, 1994; Peng *et al.*, 2004b; Babcock *et al.*, 2007, 2011). Agnostids are much more widespread with many cosmopolitan species and hence are more useful for correlation of open-shelf to shelf margin deposits (Westergård, 1946; Robison, 1976, 1984, 1994; Öpik, 1979; Peng and Robison, 2000; Ahlberg, 2003; Ahlberg *et al.*, 2004; Peng *et al.*, 2004a; Babcock *et al.*, 2007, 2011).

High resolution biozonations of Cambrian Series 3 trilobites and agnostids have been recognised on the major palaeocontinents (see Fig.1-2), with nine well established agnostid zones (in ascending order): the *Ptychagnostus gibbus*, *Acidusus atavus*, *Ptychagnostus punctuosus*, *Goniagnostus nathorsti*, *Lejopyge armata*, *Lejopyge laevigata*, *Proagnostus bulbus*, *Linguagnostus reconditus*, and *Glyptagnostus stolidotus* Zones. Some zones, such as the *G. nathorsti* and *L. armata* Zones, are not recognized on all palaeocontinents (Robison and Babcock, 2011; Babcock *et al.*, 2011). China, Russia, North America, Scandinavia, and Australia have the most complete Cambrian trilobite zonal successions. Correlation between those of South China, Siberia, North America, and Australia are shown in Figure 2. In Australia, China, Scandinavia and Russia the concept of a zone was historically based on an assemblage of species, whereas in North America it was based on the range of a characteristic

species. The recent trend is to name the regional and international zones by the FAD of the index species.

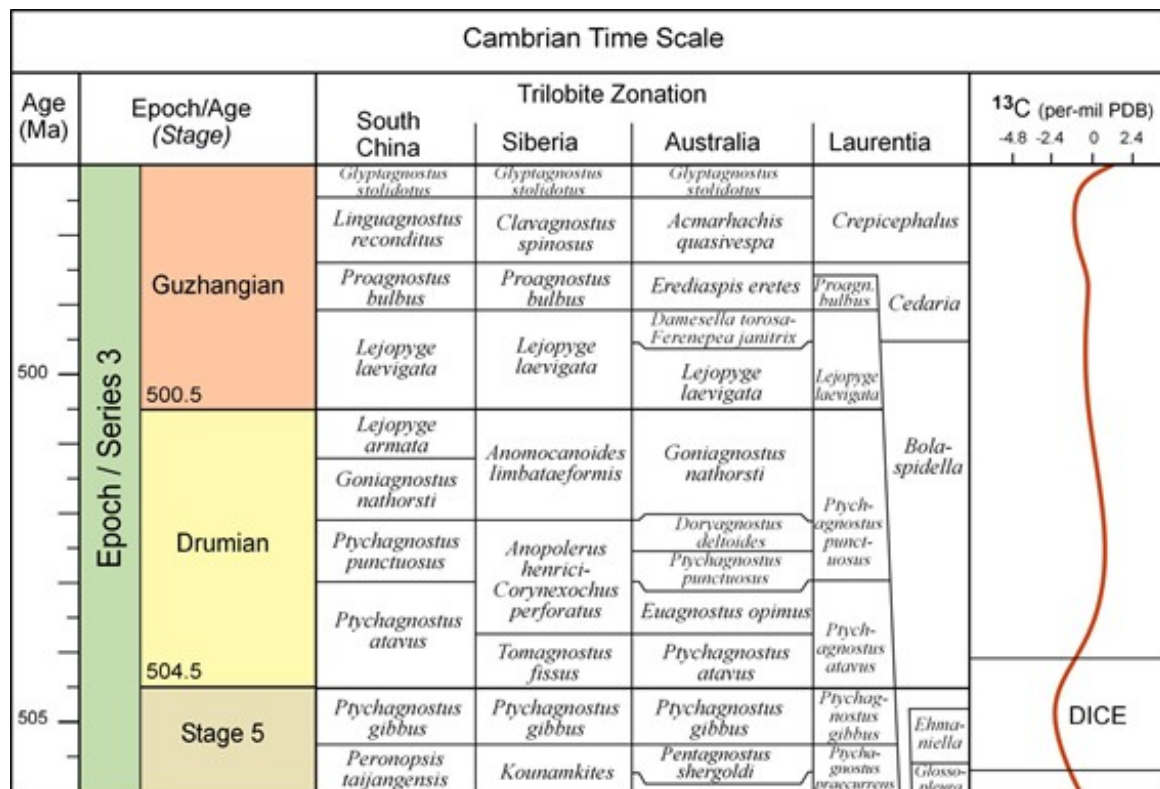


Figure 1-2. Regional biostratigraphic zonal schemes for Cambrian Series 3. The carbon isotope curve is also shown, with major named excursions (adapted from Peng et al., 2012)

1.1.2. Stage 5

The base of provisional Stage 5, also the base of provisional Series 3, is proving the most difficult of the Series 3 GSSPs to establish. The use of the first appearance datum (FAD) of an oryctocephalid trilobite to identify the base of the stage is strongly supported, with *Oryctocephalus indicus* and *Ovatoryctocara granulata*, which occurs slightly lower in section, both being proposed. Neither of these species is found in Australia although the trilobite *Bathynotus*, which is associated with *O. indicus* in places, is found in the Georgina Basin. According to ICS Guidelines on the GSSP voting procedure (Cowie et al., 1986; Remane et al., 1996), one final candidate for a boundary level should be selected, and one GSSP candidate section should be selected. This may have limited usefulness in Australia.

The three candidate sections under consideration for GSSPs are the Wuliu-Zengjiayan section of eastern Guizhou, China, the Molodo River section in Yakutia (Siberia), Russia, and the Split Mountain section in Nevada, USA. The potential GSSPs in the Wuliu-Zengjiayan and Split Mountain sections are *O. indicus* level-based, whereas the potential GSSP in the Molodo River section is *O. granulata* level-based.

Although well preserved material of *O. granulata* is also known from Greenland, Newfoundland and South China it is only common in Siberia (Yuan *et al.*, 2009) and has several other disadvantages as a global stage boundary candidate. There are questions with the definitions of both *Ovatoryctocara* Tchernysheva, 1962, and the species *O. granulata* Tchernysheva, 1962, with indications that much of the well-preserved material of *O. granulata* may represent another species (Fletcher, 2003; Yuan *et al.* 2009; Sundberg & S.C. Peng, written communication to the Lower–Middle Cambrian GSSP Working Group, September 25 and 26, 2010). Its stratigraphic range has not been studied in detail in all continents and there obviously exists a facies change between the *Ovatoryctocara* Zone (lower Amgan Stage; deeper water facies) and the underlying *Anabaraspis splendens* Zone (Toyonian Stage; shallow water facies) in the Siberian Platform.

The FAD of *O. indicus* Reed 1910, was originally proposed and accepted by the International Subcommission of Cambrian Stratigraphy (ISCS) in 2005 (Babcock *et al.*, 2005) for the Wuliu-Zengjiayan section, Guizhou, China. This proposal has been accepted by many scholars, including those from the ISCS [7, 15–19]. *Oryctocephalus indicus* was first described from the Himalayan region and is widely distributed in Korea, South China, Greenland, United States and Siberia. However, some authors have argued that *O. reticulatus* is a synonym of *O. indicus* (Zhao *et al.*, 2014). At present, the main controversy about the use of *O. indicus* as a defining mark of the base of Cambrian Series 3 concerns its geographical range.

A global distribution is key for correlation of the global boundary between Cambrian Series 2 and Series 3. The trilobite and agnostid assemblages that occur with these two candidate oryctocephalids make it possible to recognize these levels widely in most areas (Geyer, 2005). The final decision on the base of Stage 5 will depend upon investigations in the Great Basin of the U.S.A., South China and Siberia.

The base of Stage 5, as currently proposed, corresponds to a sharp, high-magnitude, negative shift in $\delta^{13}\text{C}$ values ($\geq 4\%$). This *Redlichia*-Olenellid Extinction Carbon isotope Excursion (ROECE) is one of largest negative C-isotope excursions known in the Cambrian (Zhu *et al.*, 2006). It suggests the onset of major climatic changes, which corresponds to the extinction of olenellid trilobites in Laurentia and redlichiid trilobites in Gondwana (Montañez *et al.*, 2000).

Globally, Stage 5 is subdivided into two trilobite or agnostid intervals, a lower interval of regional zones and an upper *Triplagnostus gibbus* Zone (Fig.1-2). *Triplagnostus gibbus* is a common and widespread species from all continents except Africa and South America (Öpik, 1979; Ergaliev, 1980; Ergorova *et al.*, 1982; Robison, 1982, 1984; Laurie, 1988; Young and Ludvigsen, 1989; Peng and Robison, 2000; Ahlberg *et al.*, 2003). It has been used as an index fossil in Australia, Baltica, China and Siberia (Peng *et al.*, 2012).

1.1.3. The Drumian Stage

The base of the Drumian Stage is defined by the FAD of the cosmopolitan species *Acidusus atavus*. This species is one of the most widely distributed Cambrian agnostids (e.g., Westergård, 1946; Öpik, 1979; Robison *et al.*, 1977; Ergaliev, 1980; Egorova *et al.*, 1982; Rowell *et al.*, 1982; Robison, 1982, 1984, 1994; Laurie, 1988; Geyer and Shergold, 2000; Peng and Robison, 2000; Pham, 2001; Babcock *et al.*, 2004, 2005; Ahlberg *et al.*, 2007)

being found in Australia, China, Vietnam, North Korea, Russia, Kazakhstan, Sweden, Denmark, Norway, the United Kingdom, Greenland, Canada, and the United States, and has previously been used widely as a zonal guide fossil in deposits of Baltica, Gondwana, Kazakhstan, and Laurentia (e.g. Westergård, 1946; Robison, 1976, 1984; Öpik, 1979; Geyer and Shergold, 2000; Peng and Robison, 2000; Ahlberg *et al.*, 2003, 2007). The GSSP section is located in the Drum Mountains, western Utah, U.S.A. (Peng *et al.*, 2012). The Drumian Stage was ratified by the International Commission on Stratigraphy (ICS) and the International Union of Geological Sciences (IUGS) in 2006.

Stratigraphically, the first appearance of *A. atavus* always succeeds the first appearance of *T. gibbus*, although the last appearance datum (LAD) of *T. gibbus* is commonly above the first *A. atavus* (Peng and Robison, 2000; Babcock *et al.*, 2007). In more complete successions, the LAD of *T. gibbus* falls within the lowermost part of the *A. atavus* Zone deposits of Baltica, Gondwana, Kazakhstan, and Laurentia (e.g., Westergård, 1946; Robison, 1976, 1984; Öpik, 1979; Geyer and Shergold, 2000; Peng and Robison, 2000; Ahlberg *et al.*, 2003, 2007). This interval bearing both *T. gibbus* and *A. atavus* can be recognized across the world, and allows the boundary to be tightly constrained as long as ptychagnostid-bearing strata are present in a region.

The base of the Drumian Stage corresponds to a major onset of a negative Carbon-13 excursion (Babcock *et al.*, 2007; Brasier and Sukhov, 1998) referred to as the DICE excursion (Drumian Carbon isotope Excursion) (Zhu *et al.*, 2006).

1.1.4. The Guzhangian Stage

The base of the Guzhangian Stage is recognised by the FAD of the cosmopolitan agnostid species *Lejopyge laevigata*. The GSSP lies in the Luoyixi section in northwestern Hunan, China and was ratified by the IUGS in 2007 (Peng *et al.*, 2012). *Lejopyge laevigata* is recognized on all Cambrian palaeocontinents (Westergård 1946; Cowie *et al.*, 1972; Robison, 1976, 1984; Öpik, 1979; Geyer and Shergold, 2000; Peng and Robison, 2000; Axheimer *et al.*, 2006; Peng *et al.*, 2006) and has been used as a zonal index fossil in Baltica, Gondwana, Kazakhstan, Siberia, Laurentia and Avalonia. *Lejopyge armata* and *L. calva* are also used to constrain the position of the base of the Guzhangian, with *L. armata* appearing just before the FAD of *L. laevigata* in Australia, South China, North China, Kazakhstan, Siberia and Sweden and *L. calva* the same in Laurentia. The base of the Guzhangian is above the LAD of *G. nathorsti* and below the FAD of *Proagnostus bulbus*. The FAD of *L. laevigata* also corresponds to the first appearance of damesellid trilobites such as *Palaeadotes* and *Blackwelderia* in South China and Kazakhstan (Peng *et al.*, 2013). In Australia, the FAD of *L. laevigata* defines the base of the Boomerangian stage (Öpik, 1967; Shergold *et al.*, 1985; Geyer and Shergold, 2000; Axheimer *et al.*, 2006).

1.2. Australian Biostratigraphy

1.2.1. Historical overview

The Australian stages of Cambrian Series 3 are described as “biochronological” units and are defined in terms of their constituent faunas (Shergold, 1996). The Australian scheme was pioneered by Öpik (1961, 1963, 1967, 1979) from sampling of the trilobite and agnostid faunas of surface outcrop mostly from the Georgina Basin of Queensland. However, Cambrian Series 3 outcrops in the Georgina Basin provide few extensive sections suitable for biostratigraphic analysis. Öpik correlated the agnostid faunas from these spot localities in

the Georgina Basin with the Scandinavian faunas described by Westergård (1946), which worked reasonably well due to the considerable number of cosmopolitan species. However, Öpik's scheme relied on the presence of these cosmopolitan species or the interpretation of the surrounding stratigraphy. In many Cambrian Series 3 localities in Australia this stratigraphy is poorly documented or understood (Laurie, 2006).

1.2.2. Stage 5 in Australia

Recent work on agnostid and trilobite faunas by Laurie (2004, 2006, 2012a,b) in the Georgina Basin of Queensland and the Northern Territory and Kruse *et al.* (2004) in the Ord Basin of Western Australia, has culminated in a refined definition of Stage 5 in Australia (Laurie, 2012). The Ordian, originally proposed by Öpik (1968) to represent a time-division based on the occurrence of the *Redlichia chinensis* faunal assemblage, is now understood to be approximately coeval with the upper portion of Stage 4 in Cambrian Series 2 – the upper part of the traditional Lower Cambrian. This has been recently suggested by several workers (Brock and Percival, 2006; Paterson and Brock, 2007; Kruse *et al.*, 2009). The overlying Templetonian is considered to be almost equivalent to Stage 5, rather than being divided into an 'early Templetonian' (united with the Ordian) and a 'late Templetonian' (united with the Drumian Stage) as had previously been considered (Shergold, 1989, 1996). The current biostratigraphic scheme is shown in Figure 1-3. It places the base of Stage 5 with the FAD of *Pentagnostus krusei*. It is unclear how this relates to the FAD of *Oryctocephalus indicus*, one of the candidates for the global Stage 4-Stage 5 boundary, because that species has not yet been found in Australia. The Templetonian, which comprises the majority of Stage 5, is redefined to include (in ascending order): the *Pentagnostus anabarensis*, *P. praecurrens*, *P. shergoldi* and *Triplagnostus gibbus* Zones (Laurie, 2004, 2006). Chapter 3 herein shows the presence in the *T. gibbus* Zone of Australia of cosmopolitan agnostid species such as

Peronopsis amplaxis, *Onymagnostus semiermis*, *Rhodotypiscus nasonis*, *Goniagnostus lemniscatus* and *Euagnostus interstrictus* – all useful for international correlation.

C A M B R I A N																
Series 2		Series 3														
Stage 4		Stage 5			Drumian			Guzhangian								
Ordian		Templetonian			Floran	Undillan		Boomerangian	Mindyallan							
												Lejopyge laevigata	IV	Erediaspis eretes	Amarhachis quasivespa	Glyptagnostus stolidotus
													III			
													II			
I	Goniagnostus nahorsti	Doryagnostus deltoides	Ptychagnostus punctuosus	Euagnostus opimus	Acidusus atavus	Triplagnostus gibbus	Pentagnostus shergoldi	Pentagnostus praecurrens	Pentagnostus andbarensis	Pentagnostus krusei	Xystridura negrina	Redlichia jorressi				

Figure 1-3. Australian Stage and zonal subdivisions of Cambrian Series 3 (adapted from Fig. 2, Laurie, 2012)

Note: *Lejopyge laevigata* IV Zone replaces Öpik's (1967, 1979) *Damesella torosa-Ascionepea janitrix* Zone of Passage.

1.2.3. Drumian in Australia

In Australia, the Drumian Stage is divided into an earlier Floran Stage and a later Undillan Stage. The concept of the Floran was revised by Shergold (1995) who combined it with the late Templetonian Stage due to the range overlap of *T. gibbus* and *A. atavus* in the Georgina Basin. By redefining the Templetonian Stage, the base of the Floran has been restored to its original proposed level (Laurie, 2004, 2006; Kruse *et al.*, 2009). Öpik (1970) divided the Floran stage into two agnostid zones – a lower '*Ptychagnostus*' *atavus* Zone and an upper *Euagnostus opimus* Zone (see Fig. 2). Although he did not formally define the *Acidusus atavus* Zone, Öpik placed *Ptychagnostus* (to which he assigned *A. atavus*) as appearing a short distance above the base of the Floran (Öpik 1979, table 2), and hence the base of the *A.*

atavus Zone, making his meaning of the *A. atavus* Zone unclear (Laurie, 2004). The base of the *Acidusus atavus* Zone is defined at the first appearance of *A. atavus* (see Fig. 3). Öpik (1979) recorded 23 agnostid species in the *A. atavu* Zone, which is characterized by the earliest diplagnostids, the ascendancy of the *Goniagnostus* lineage, the first *Hypagnostus* and a distinctive association of genera including *Triplagnostus*, *Rhodotypiscus*, *Goniagnostus*, *Iniospheniscus* and *Zeteagnostus* (Shergold, 1996). Öpik (1979) replaced the *H. parvifrons* Zone in the Swedish scheme with that of *E. opimus* (Laurie, 2004), due to the sparse occurrence of *H. parvifrons*. The taxonomy of *E. opimus* has been questioned by Jell and Robison (1978) and Peng and Robison (2000), with Laurie (2012a) reassigning several specimens to *Doryagnostus* due to the incorrect assignment of cephalae and pygidia. The present work documents the presence of *H. parvifrons* in the Gowes Formation of the Georgina Basin, allowing a re-evaluation of this portion of the Australian Cambrian biostratigraphic scheme. Due to the long range of *H. parvifrons*, Høyberget and Bruton (2008) included the *H. parvifrons* Zone in an extended *A. atavus*

Zone for sections in Norway, as did Weidner and Nielsen (2009, 2013) for the Mörbylilla Member of the Alum Shale Formation of Sweden. This portion corresponds to the *Hypagnostus parvifrons* zone *sensu* Westergård 1946. This terminology was also adopted by Axheimer and Ahlberg (2003). The occurrence of *H. parvifrons* in this present study occurs at the same stratigraphic level occupied by *Hypagnostus parvifrons* in the European biostratigraphic scheme (Høyberget and Bruton, 2008; Weidner and Nielsen, 2009, 2013). The base of the Floran coincides with the base of the global Drumian Stage, the base of the Wangcunian Stage of South China, and the base of the Marjuman Stage of North America (Babcock *et al.*, 2007).

The Undillan sub-stage, above the Floran, was divided by Öpik (1979) into the lower *Ptychagnostus punctuosus* Zone and upper *Goniagnostus nathorsti* Zone. These zones contain cosmopolitan agnostid genera such as *Svenax*, *Baltagnostus*, *Doryagnostus*, *Myrmecomimus* and *Oedorhachis* (sensu Öpik) as well as species with earlier origins, of *Pseudoperonopsis*, *Acidusus*, *Aristarius*, *Onymagnostus*, *Euagnostus*, *Aotagnostus* and *Doryagnostus*. Characteristic trilobites are ptychoparioids, anomocarids, mapaniids and damesellids, conocoryphids, corynexochids, nepeids and dolichometopids.

1.2.4. Guzhangian Stage in Australia

In the traditional Australian scheme, the Guzhangian Stage is divided into an early Boomerangian Stage and a later Mindyallan Stage. The Boomerangian consists of the *Lejopyge laevigata* Zone, which Öpik (1979) subdivided into *L. laevigata* I, II and III on the basis of distinct trilobite assemblages (see Fig. 3). *Delagnostus* is the only agnostid confined to the Boomerangian, but characteristic species of *Lejopyge*, *Hypagnostus*, *Grandagnostus*, *Oidalagnostus* and *Diplagnostus* are accompanied by the trilobites *Centroleura*, dolichometopids, olenids, mapaniids, corynexochids and damesellids (Peng *et al.*, 2012).

Öpik (1963) originally proposed the Mindyallan Stage to include a “pre-*Glyptagnostus stolidotus*” Zone and a *G. stolidotus* Zone, but later revised this (Öpik, 1966, 1967) in establishing three zones (in ascending order): the *Erediaspis eretes*, *Acmarrhachis quasivespa* (under the name of *Cyclagnostus quasivespa*) and *G. stolidotus* Zones. The *E. eretes* Zone contains 27 trilobite genera belonging to anomocarids, asaphiscids, catillicephalids, damesellids, leiostegiids, lonchocephalids, menomoniids, nepeids, norwoodiids, rhyssometopids, and tricrepicephalids. Eighteen species of trilobites are confined to the *A. quasivespa* Zone, but many other species range into it from lower zones (Peng *et al.*, 2012). Daily and Jago (1975) subdivided the *A. quasivespa* Zone into two assemblages based on the

occurrence of *Lejopyge armata* and *Blackwelderia sabulosa*. Only eight species range from the *A. quasivespa* Zone into the overlying *G. stolidotus* Zone. The *G. stolidotus* Zone contains 75 trilobite species that have Laurentian (e.g., asaphiscids, auritamids, catillicephalids, norwoodiids, and raymondinids) and Chinese (e.g., damesellids and liostracinids) affinities; this is discussed in greater detail in Chapter 4.

1.3. Taxonomic Revision of Georgina Basin agnostids and trilobites

Many biostratigraphical units of the Georgina Basin are still undefined or poorly calibrated with geochronological tie points (Young & Laurie, 1996; Brock *et al.*, 2000). Much of the Australian Cambrian timescale is underpinned by the taxonomy and biostratigraphy of the agnostids and trilobites, and in many cases this was based on spot samples from the Georgina Basin. Thus, there is uncertainty with regard to the reliability of zonations, as taxon ranges are often poorly constrained.

Öpik distinguished trilobite and agnostid genera and species using variations in linear and non-linear characters. Some of these variations are most likely due to ontogenetic or morphological variation, geographic variation or represent different modes of preservation. Traditionally, morphometric statistical analysis has not been practiced widely in trilobite taxonomy and combined with a lack of stratigraphic control, has resulted in many Australian species and genera being in need of a modern systematic treatment.

This current work re-evaluates and revises 17 agnostid and trilobite taxa from the Georgina Basin, many of which have been previously documented by Öpik (1979), Jell and Robison (1978) and Laurie (2004, 2006). The taxonomy is based on new and existing collections, allowing refinement of the Templetonian-Drumian portion of the Australian timescale and

better intra- and intercontinental correlation. More reliable data has also been obtained for a large biogeographic analysis.

1.3.1. Revision of the trilobite *Rhyssometopus*

Many trilobite and agnostid species of Australian Cambrian Series 3 have been differentiated on small variations in their characteristics, without consideration of ontogenetic or morphological continua, mainly due to the lack of well-preserved specimens. Descriptions are often based on isolated and poor specimens. This lack of precision in taxonomy may result in an overabundance of species, a lack of recognition of morphological/ontogenetic differences and an eventual failure to reach the most appropriate evolutionary conclusions. Precision in taxonomy is dependent on the choice of the correct characters and statistical methods. The *Rhyssometopus* trilobite is one case of a lack of precision in determination of the various species, resulting in more species than was necessary and a lack of recognition of morphological variation. Chapter 2 presents a morphometric analysis of the Cambrian Series 3 (Guzhangian) species of the trilobite *Rhyssometopus* from northwestern Queensland. Bivariate analysis is conducted to detect both inter- and intraspecific variability of the morphological dimensions. Results demonstrate that the four species *Rhyssometopus rhyssometopus*, *R. princeps*, *R. rugiceps* and *R. neuter* cannot be differentiated on the basis of linear dimensions previously used by Öpik (1967) as diagnostic characters. Nonlinear characters are found to be more reliable for differentiating the species of *Rhyssometopus*. The type species, *R. rhyssometopus*, is considered a senior subjective synonym of *R. princeps* and *R. rugiceps*. The erection of the subgenus *Rostrifinis* was found to be unwarranted. The occurrence of all *Rhyssometopus* species from Australia, Antarctica and China was reviewed, and emended diagnoses provided for the following valid species: *R. rhyssometopus* Öpik, 1967, *R. neuter* Öpik, 1967, *R. nitidus* Duan, 2004, *R. rostrifinis* Öpik, 1967, *R. thielei*

(Chapman, 1911), and *R. zhongguoensis* Zhou, 1977. The family Rhyssometopidae consists of the genera *Rhyssometopus*, *Plectrifer*, *Qiandongaspis* and *Tasmana*.

See Chapter 2: The Cambrian trilobite *Rhyssometopus*, with taxonomic revision of Guzhangian species from Queensland, Australia.

1.3.2. Ptychagnostidae taxonomy

The family Ptychagnostidae Kobayashi, 1939, in particular has suffered from extensive problems in taxonomy due to interpretations of morphological and geographical variation. Laurie (1988) details the problems with the usage of morphological features such as length and width of the exoskeleton, which have resulted in long synonymy lists for the various species (see Robison, 1982, 1984). Robison's approach is in opposition to that used by Öpik (1979) who erected 15 genera and subgenera based on similar morphological criteria, some of which can be shown to vary intraspecifically (Laurie, 1988). Laurie (1988) condensed these 15 genera to 12 genera, more than the five genera originally assigned by Robison (1982, 1984). The taxonomic interpretations of Laurie (1988) are followed herein.

The Gowers Formation of western Queensland in the Georgina Basin contains large numbers of well-preserved specimens of ptychagnostids, specifically *Goniagnostus lemniscatus*, *Onymagnostus semiermis*, *Triplagnostus gibbus* and *Zeteagnostus sinicus*, allowing identification of morphological and ontogenetic variations and more thorough descriptions of these species. Complete specimens of *G. lemniscatus* are illustrated for the first time, exceptionally preserved specimens of *O. semiermis* presented and juvenile specimens of *T. gibbus* from the lower *Acidusus atavus* Zone. The information from the Gowers specimens contributes to our understanding of the evolution of ptychagnostids.

Although in very low numbers, the ptychagnostid species *Tomagnostus fissus* is found in Australia for the first time.

See Chapter 3: Trilobites and agnostids from the Gowers Formation (Cambrian Series 3), Georgina Basin, Queensland, Australia. “The Biostratigraphy of the Cambrian Series 3 Gowers Formation, Georgina Basin, Queensland, Australia.

1.4. Agnostids and trilobites of the Gowers Formation of the Georgina Basin: Implications for the Australian Cambrian timescale and global correlation

The Gowers Formation of the southern Georgina Basin of western Queensland was defined and described by Southgate (1983, 1986a) for the phosphatic interval originally assigned to the basal part of the Currant Bush Limestone. The Gowers Formation contains exceptionally preserved shelly faunas, with agnostids, trilobites, bradoriids, brachiopods, molluscs, palaeoscolecids, echinoderm fragments, conodonts, chancelloriids and various other ‘small shelly fossils’ having been previously described (e.g. Jell, 1975; Jell & Robison, 1978; Runnegar & Jell, 1976; McKenzie & Jones, 1979; Öpik, 1979; Jones & McKenzie, 1980; Shergold, 1991; Walossek et al., 1993; Müller & Hinz-Schallreuter, 1993; Paterson, 2005; Vendrasco et al., 2010; Moore, 2013). Southgate (1986a) considered the formation to be *E. opimus* Zone in age, based mainly on fossil data from Jell (1975) and Öpik (1979), with subsequent authors accepting this age determination.

This study is based on extensive fossil collections from two comprehensively sampled sections of the Gowers Formation, permitting a detailed systematic description of the trilobite and agnostid faunas and in turn, a more accurate age for the unit. Results show that the faunas range from the *Triplagnostus gibbus* Zone to lower *Acidusus atavus* Zone, straddling the Stage 5 to Drumian boundary and the global Drumian Carbon isotope Excursion (DICE). The

stratigraphic interval from the late *T. gibbus* Zone to the lower *A. atavus* Zone is narrow but widely recognizable if ptychagnostids are present (Babcock *et al.*, 2007). A combination of agnostids and trilobites allows for precise correlation globally. Age-diagnostic taxa include the cosmopolitan agnostid species *Euagnostus interstrictus*, *Onymagnostus semiermis*, *Triplagnostus gibbus*, *Peronopsis amplaxis* and *Hypagnostus parvifrons*, allowing a more precise correlation with Baltica, Siberia, Laurentia and South China. Due to the presence of *Hypagnostus parvifrons* in Australia, plus the doubtful nature of the taxonomy of *E. opimus* in Australia, this study recommends that the *E. opimus* Zone should be replaced by the “upper *A. atavus*” Zone to correlate with recent changes to the Swedish scale (Weidner and Nielsen, 2013).

Faunal assemblages in the Gowers Formation are found to correlate most closely with those of from the Arthur Creek Formation in the Georgina Basin (Laurie, 2004, 2006) and Nevada and Utah, U.S.A. (Robison, 1964, 1982, 1984, 1995), Norway (Hoyberget and Bruton, 2008) and Sweden (Axheimer and Ahlberg, 2003; Weidner and Nielsen, 2009).

1.5. Palaeobiogeographic setting of East Gondwana during Cambrian Series 3

1.5.1. Historical palaeobiogeography

Classical palaeobiogeographical analyses led to the subdivision of palaeocontinents into faunal realms, regions and provinces. Despite a lack of consistent definition of such terms as ‘region’ and ‘province’ in palaeontology, the syntheses have been useful for a better understanding of the appearance and disappearance of biogeographical barriers (commonly related to the rifting and drifting of major tectonostratigraphic units; e.g. Burrett and Richardson, 1980; Torsvik *et al.*, 1996; Zhao *et al.*, 1996) and latitude- or depth-related thermal gradients. Over recent decades, a huge quantity of new trilobite and agnostid data

have assisted biogeographical interpretation but many tectonic configuration models remain equivocal. Consequently, quantitative methods for analyses of spatial and temporal distribution of Cambrian trilobites and agnostids have taken on a larger role in recent times. This present study uses multivariate analyses of trilobite and agnostid genera to refine the placement of East Gondwana in a global palaeobiogeographical context during Cambrian Series 3 (see **Chapter 4: Biodiversity, biofacies and biogeography of middle Cambrian (Series 3) arthropods (Trilobita and Agnostida) on the East Gondwana margin.**

1.5.2. Cambrian Series 3 biogeography of the East Gondwana margin

The biogeographic context of East Gondwana during Cambrian Series 3 has mostly been studied at a global and/or Series scale (Zhang, 1989; Jell and Hughes, 1997; Zhang, 1998; Hughes and Jell, 1999; Peng *et al.*, 2009; Álvaro *et al.*, 2013; Weidner and Nielson, 2013). However, Jell (1974) used trilobite genera and families to divide the Middle Cambrian into three provinces: Columban, Viking and Tollchuticook, with the latter province consisting of Australia, Asia and Antarctica. Burrett and Richardson (1980) used multivariate analysis of trilobite and agnostid assemblages to achieve similar results to Jell's (1974), although with slightly weaker China- Australian connections.

A lack of definition of palaeobiogeographical terms has made it difficult to compare different palaeogeographic units using global Cambrian trilobite genera. Alvaro *et al.*, (2013) discuss the different tectonostratigraphic units of the Cambrian as: Laurentia, Baltica, Siberia, West Gondwana terranes, East Gondwana (Iran, Afghanistan, central Asia, the Himalayan region, Thailand, Vietnam, China, Australia, New Zealand and Antarctica), Avalonia, Cuyania, Ossa–Morena, Chinese domains, Alai terrane (Turkestan), Kazakhstani island arcs and terranes. These are followed in this study.

During the Cambrian Series 3, the ~ 6000 km-long East Gondwana margin stretched from northern Australia to the Transantarctic Mountains of Antarctica, encompassing what is now mainland Australia, western Tasmania, New Zealand and eastern Antarctica (Brock *et al.*, 2000; Li and Powell, 2001; Boger and Miller, 2004; Squire and Wilson, 2005; Federico *et al.*, 2009; Cayley, 2011). This region of East Gondwana was situated in an equatorial position, with the margin in an approximately NW–SE orientation (Brock *et al.*, 2000; Li and Powell, 2001; Torsvik and Cocks, 2013) Based on the trilobite and agnostid faunas of the three stages of Series 3, this study finds very strong connections of East Gondwana with South China, reinforcing assertions by some that the South China plate was very close to the west Australian margin (Torsvik and Cocks, 2013; Weidner and Nielsen, 2013)

Chapter 4 of this thesis presents the first quantitative biogeographic and diversity analyses of Cambrian Series 3 trilobite and agnostid assemblages from the East Gondwana margin, building on work by Brock *et al.* (2000) and Gravestock and Shergold (2001), and complementing similar studies on Cambrian trilobites and agnostids from West Gondwana (Álvaro *et al.*, 1999, 2003). Taxonomic and biostratigraphic data on many East Gondwanan fossil assemblages has increased and improved greatly over recent years, and taxonomic synonymies of many species for this chapter were checked by J. Jago and J. Laurie. All documented trilobite and agnostid synonymies from Jell and Adrain (2003), Synplus and Index to Organisms (ION) were incorporated and personal interpretation was used on a few occasions. One trilobite genus was renamed in the process – “*Eurostinella*, a new generic replacement name for *Eurostina* Curran, 1932 (Diptera) (Pro *Eurostina* Whitehouse, 1939 (Trilobita), preoccupied)”.

Three extensive datasets of generic occurrences were compiled for each of the three stages of the Cambrian Series 3 (Stage 5, Drumian and Guzhangian). Analyses by various multivariate

and parsimony methods revealed dynamic patterns and relationships between the East Gondwanan sites, reflecting an extensive complex of depositional settings and biofacies along the margin. These biogeographic patterns, as well as diversity trends are documented across all stages and matched to recently published global sea level curves (e.g., Haq and Schutter, 2008; Peng *et al.*, 2012). East Gondwana diversity trends are also compared with previously recorded patterns of Cambrian Series 3 trilobites and agnostids from other regions (e.g., Burrett and Richardson, 1978; Álvaro *et al.*, 1999, 2003; Zhen and Zhou, 2007; Ergaliev *et al.*, 2008; Zhen and Zhou, 2008).

1.5.3. Cambrian Series 3 trilobite and agnostid assemblages from the East Gondwana margin

The East Gondwana margin contains almost 23% of Cambrian Series 3 trilobite and agnostid genera known worldwide, with close biogeographic ties with North and South China, the Himalaya, and to a lesser extent, Iran, Kazakhstan, Laurentia and Siberia. East Gondwanan trilobite and agnostid faunas show an overall increase in generic diversity throughout Cambrian Series 3, reaching a sharp peak in the Guzhangian. These major diversifications most likely correspond to eustatic transgressive phases, as documented for other parts of the world in the Drumian (Babcock, 2006, 2007; Haq and Schutter, 2008; Fatka *et al.*, 2011; Peng *et al.*, 2012) and the Guzhangian (Haq and Schutter, 2008; Peng *et al.*, 2009, 2012). The diversity trends for the East Gondwana margin is found to match that for contemporaneous faunas in other parts of the world, especially in China (Zhen and Zhou, 2007, 2008), Kazakhstan (Ergaliev *et al.*, 2008) and West Gondwana (Álvaro *et al.*, 1999, 2003), although diversity in the latter region reaches an acme in Drumian times. The diversification in the Drumian coincides with the tectonic development of island arc systems outboard of the southern East Gondwana margin (Münker and Cooper, 1999; Cawood *et al.*, 2009; Federico *et al.*, 2009) and the connection of mainland basins and shelves (Moore *et al.*, 2013).

Stage 5 faunas were found to be largely restricted to mainland Australia and to represent deep water, outer shelf biofacies that commonly contain the agnostids *Acadagnostus* and *Itagnostus*, oryctocephalids, *Pagetia* and *Xystridura*. Drumian faunas inhabited a wide range of palaeoenvironments along the margin, from intertidal and subtidal settings to deep water, low oxygen, outer shelf settings. Guzhangian faunas are represented along the entire East Gondwanan margin with a large proportion representing assemblages from outer shelf to slope biofacies, including a large number of eurytopic agnostid species. The profusion of cosmopolitan agnostid species in association with distinct deep water trilobite-agnostid biofacies along the entire East Gondwana margin strongly reflects the eustatic transgressive event that reached its pinnacle during the Guzhangian, allowing for greater faunal exchange between areas on the margin and other parts of the world.

This study was the first large biogeographic and diversity study of Series 3 on the East Gondwana margin and the results suggest that further research on the following would be highly desirable:

1. Documentation of poorly known/documented trilobite and agnostid assemblages such as those from the Coonigan Formation (Gnalta Shelf of New South Wales), the Knowsley East Shale (Victoria), the Kalladeina Formation (Warburton Basin), the Molar Formation (Northern Victoria Land, Antarctica) and the Amadeus Basin.
2. Modern systematic revisions of key trilobite and agnostid groups.
3. Biofacies case studies on specific faunas, including relative abundance data and detailed facies analysis.

4. Construction of a comprehensive dataset for the Furongian of the East Gondwana margin

These data would present a more comprehensive picture of the global biogeography and diversity trends of Cambrian trilobites and agnostids during the zenith of their evolutionary history.

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Chapter 2. The Cambrian trilobite

***Rhyssometopus*, with taxonomic revision of Guzhangian species from Queensland, Australia**

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Chapter 3. The Cambrian Series 3 Gowers Formation of the Georgina Basin

Outcrops of the richly fossiliferous Gowers Formation in the northwestern Queensland of the Georgina Basin present an excellent opportunity to study the contained agnostid and trilobite fauna to improve our understanding of Australian biostratigraphy and sequence stratigraphy for Cambrian Series 3. This knowledge provides a valuable addition to recently refined global biostratigraphic schemes for the Cambrian Period (Peng *et al.*, 2012; Laurie, 2006, 2012). The Gowers Formation has a diverse, exceptionally preserved macro- and microfossil assemblage (Shergold and Laurie in Shergold and Southgate, 1986), including a rich molluscan fauna (Runnegar and Jell, 1976; Kruse, 2002; Vendrasco *et al.*, 2010, 2011). However, it is the agnostid faunas which are proving to be excellent biostratigraphic indicators for this time interval of the Cambrian Period. Agnostid diversity reached its maximum during Series 3 and, due to their abundance, wide geographic distribution and relatively rapid evolution, are the best means of correlating Series 3 strata globally (Ahlberg, 1989). Many agnostid species have global distributions in open-marine lithofacies (Peng & Robison, 2000), allowing accurate intercontinental correlation.

The trilobites and agnostids, brachiopods, bradoriids, echinoderm fragments, conodonts, chancelloriids and various tubes and spines in the Gowers Formation (Shergold and Laurie in Shergold and Southgate, 1986) show exceptional preservation, with many microfossils occurring as phosphatic moulds or casts (Runnegar 1985). The faunal elements that have been previously described from the Gowers Formation include: brachiopods (Henderson and MacKinnon, 1981); bradoriids (Jones and MacKenzie, 1980); molluscs (Runnegar and Jell, 1976, 1980; Runnegar, 1985; Kruse, 2002; Vendrasco *et al.*, 2010, 2011); trilobites (Paterson, 2005).

Although many of these faunal elements of the Gowers Formation have been previously collected and described in detail, the biostratigraphic knowledge is poor as previous trilobite and agnostid descriptions, other than those of Paterson (2005), were based on spot collections and often on too few or poorly preserved specimens. Öpik & Pritchard (1960, fig. 14) indicated that the base of the Currant Bush Limestone, to which the phosphatic rocks of the Gowers Formation were assigned prior to their formal documentation in 1986, began just above the base of the *Triplagnostus gibbus* Zone. Yet Öpik (1979) indicated specimens found at localities in the basal Currant Bush Limestone (= Gowers Formation), should be assigned an *Euagnostus opimus* age. Southgate (1986a) suggested an *E. opimus* Zone age for the Gowers Formation, based on the faunal data of Jell (1975) and Öpik (1979), although Jell (1975) relegated some samples to the underlying *Acidusus atavus* Zone as well. A complete taxonomic and biostratigraphic evaluation has now been undertaken in this study.

A thorough taxonomic treatment and evaluation of the agnostid and trilobite faunas from two finely sampled sections of the Gowers Formation is performed herein, and are indicative of a *Triplagnostus gibbus* Zone to lower *Acidusus atavus* Zone age. The new proposed Australian agnostid zonation for Cambrian Series 3 of Laurie (2012) is followed here, with the most recent inclusion of the *Hypagnostus parvifrons* Zone in an upper *A. atavus* Zone (following Høyberget and Bruton, 2008; Weidner and Nielsen, 2009, 2013) also adopted. The age evaluation is mainly agnostid-based, as agnostid species dominate the fauna, with many species having a global distribution and/or a restricted range. Trilobite species tend to be more restricted in their global distribution and all five species from the Gowers Formation are endemic to East Gondwana. Thirteen species of agnostids and five trilobite species are described, including one new species. Illustrated specimens were chosen to show the intraspecific (including ontogenetic) variation of the species. The Gowers Formation fauna is

found to be most like those from Cambrian Series 3 of Laurentia and Baltica, showing closest similarities to faunas from Sweden (Westergård, 1946; Weidner and Nielsen, 2013; Axheimer and Ahlberg, 2003), Norway (Høyberget and Bruton, 2008), Denmark (Berg-Madsen, 1984), North Greenland (Robison, 1994) and the United States (Robison, 1982, 1984).

3.1. Geological Setting: The Georgina Basin

The Georgina Basin is a large Proterozoic to Palaeozoic sedimentary basin covering an area of approximately 325 000 km² in northwestern Queensland and eastern central Northern Territory (Smith, 1972; Shergold and Druce, 1980; Laurie, 2004, 2006; Dunster *et al.*, 2007). It represents an erosional remnant of a more extensive Neoproterozoic to Cambrian Centralian Superbasin of central and northern Australia. It contains up to 600 m of Neoproterozoic clastics with minor carbonate and 5000 m of Cambrian, Ordovician and Devonian clastics and carbonates. The most complete successions occur along the eastern and southern margins of the basin, with the Palaeozoic succession thickest near the southern margin and rarely exceeding 400 metres in the north (Laurie, 2006). The basin was mildly deformed during the Alice

Springs Orogeny (Middle Devonian – Early Carboniferous) through minor to moderate folding and faulting, particularly to the south and east with moderate to severe folding, faulting and overthrusting along the southern margin (Freeman *et al.*, 1990). Numerous petroleum exploration wells have been drilled in the basin (Questa Australia Pty Ltd, 1994) as several of the southern Georgina Basin units of Cambrian Series 3 age have shown the potential for economic petroleum accumulations. In 1999, the Northern Territory Geological Survey (NTGS) initiated a project to improve the understanding of the structure, stratigraphy and regional petroleum systems of the southern part of the basin. The Cambrian Series 3 succession of the Georgina Basin was recognized as significant in the search for

sedimentary phosphorites by the B.M.R. in the 1960s and by Sheldon (1966) (Russell and Trueman, 1971). The basin currently contains the majority of Australia's phosphate resources. However, despite this extensive research effort in the Georgina Basin, many biostratigraphical units remain undefined or poorly calibrated with geochronological tie points (Young & Laurie, 1996; Brock *et al.*, 2000).

During Cambrian Series 3 time, central Australia was periodically invaded by a broad epeiric sea (Cook, 1982; Southgate, 1983, 1986b), which resulted in widespread sedimentation in the Georgina Basin and the Wiso, Daly, Ngalia, Amadeus and Ord Basins. Cook (1982) and Southgate (1983) suggested that a westerly-directed equatorial current was probably deflected in a northwesterly direction as it approached the continent; see Chapter 4 for more detail on Australia's position during Cambrian Series 3). The Georgina Basin was most likely a large epicontinental sea with shallow embayments and restricted access to the palaeo-Pacific Ocean (Russell and Trueman, 1971; Cook, 1982; Hally and Paterson, 2014).

3.1.1. The history of Cambrian stratigraphic and palaeontologic investigations in the Georgina Basin

Brown (1895, 1897, 1903) found the first documented Cambrian trilobites near Alexandria in the western section of the basin, which were documented and analysed by Etheridge (1897). Davidson (1905) collected Cambrian trilobites near Elkedra (documented and analysed by Etheridge, 1902) and Madigan's expeditions (1929, 1932, 1937) first recorded the geology of the southwestern part of the Georgina Basin. Middle Cambrian trilobites were described by Chapman (1929) and Whitehouse (1936, 1939, 1945). The earliest systematic work began about 1950 when the Bureau of Mineral Resources (BMR) commenced a regional mapping program (Öpik 1956, 1960; Smith 1972). The program led to the publication of a series of 1:250 000 geological maps of the entire Georgina Basin, and a monograph of the geology of

the basin by Smith (1972). Palaeontological investigations of the Queensland material were carried out simultaneously by Öpik (1956, 1958, 1960, 1961, 1963, 1967, 1970, 1975, 1979), Jell (1975, 1978) and Jell and Robison (1978). A limited amount of drilling occurred in the basin in the 1960s and 1970s by Questa Australia Pty Ltd (1994) in the search for petroleum in Cambrian Series 3 rocks. The discovery of phosphorites also resulted in renewed interest in the late 1960s and 1970s, leading to biostratigraphical work by Shergold (1969, 1972, 1979), Fleming (1974), Shergold and Druce (1980), Cook (1989) and others. Shergold (1985), Shergold and Walter (1979), Walter *et al.* (1979), and Walter (1980) documented aspects of the stratigraphy and palaeontology of the southern Georgina Basin, including early Cambrian acritarchs and trace fossils from the Desert Syncline. The Northern Territory Geological Survey (NTGS) undertook a regional mapping program in the early 1980s, remapping several 1: 250 000 map sheets of the western Georgina Basin (e.g. Freeman, 1986; Stidolph *et al.*, 1988). Southgate and Shergold (1991) undertook a sequence stratigraphic analysis of the Georgina Basin in conjunction with several phosphate projects. Ambrose *et al.* (2001) revised the lithostratigraphy of the southern Georgina Basin, proposing new and improved stratigraphical relationships based on subsurface mapping and depositional history.

3.1.2. The Gowers Formation

Named after the nearby Gowers Bore, the Gowers Formation was defined and described by Southgate (1983, 1986a). Prior to this, rocks of the Gowers Formation were considered to be the phosphatic sediments at the base of the Currant Bush Limestone. Major palaeontological studies by Jell (1975) and Öpik (1979) did not recognize this unit. The unit consists of limestone, phosphatic limestone, phosphorite and its diagenetic equivalents (Southgate, 1983). The extent of outcrop is shown in Fig.3-1. The designated type section,

Section 418, is located about 6 km SSW of Thornton Station (see section on Methods for detail of locality). The unit is delineated by a lower disconformable surface at the boundary with the underlying Bronco Stromatolith Bed, which forms the upper unit of the Thornton Limestone, and an upper disconformable surface which separates the Gowers Formation from the overlying Currant Bush Limestone. Detailed lithology is given by Southgate (1983) and only a summary is given below.

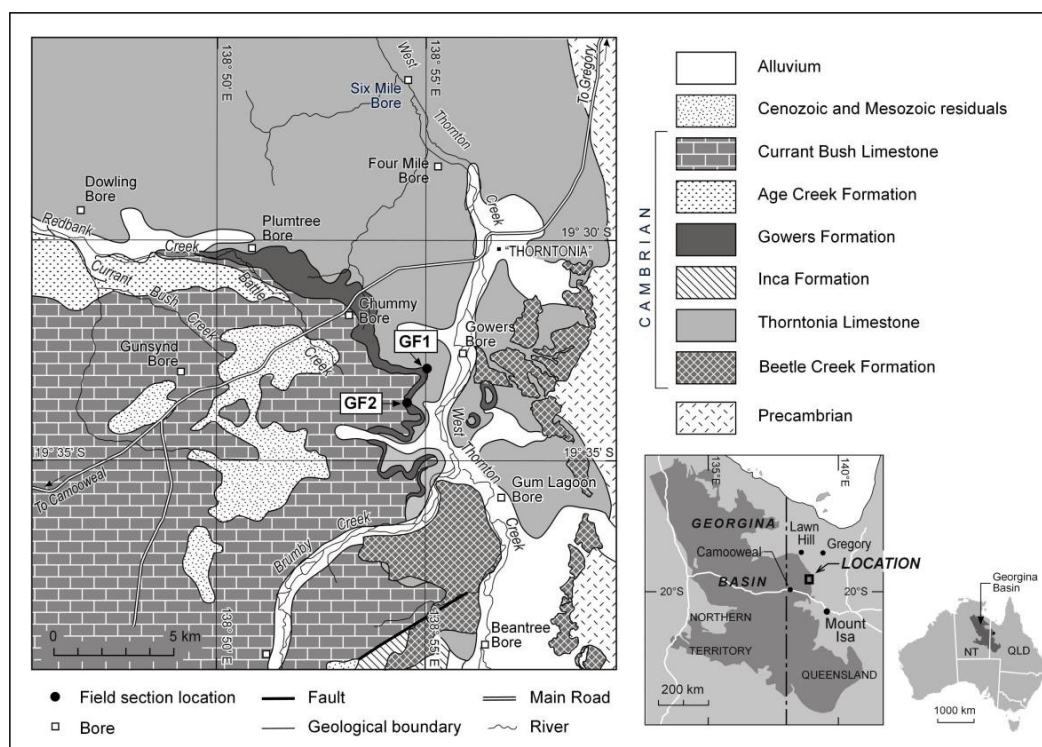


Figure 3-1. Geological location map of sections GF1 (Type Section 418) and GF2, Gowers Formation, Georgina Basin, northwestern Queensland.

3.1.3. Lithology of the Gowers Formation

Southgate (1983, 1986a) outlined the change in lithologies from east to west of Chummy Bore, with the east being mostly bituminous limestone, phosphatic limestone and chert, and the west containing more dolostone that is phosphatic in parts. Above the Bronco Stromatolith Bed, the basal rocks of the Gowers Formation are phosphatic dolostones which pass vertically into mostly non-phosphatic dolomitic limestones and limestones that contain interbedded chert nodules. The rocks are predominantly calcareous mudstone and

wackestone. Subordinate calcareous packstone phosphorites and coquina grainstone also occur. Phosphatic mudstones and wackestones occur in normally graded thin beds and laminae, or have a bioturbated texture. Minor occurrences of barite and fluorite occur in the phosphatic limestones and dolostones. The distribution of phosphate grains is what distinguishes the rocks of the Gowers Formation from the overlying Currant Bush Limestone. The Gowers Formation contains phosphate grains of both skeletal and non-skeletal origin, while the Currant Bush Limestone only contains skeletal grains of brachiopods and bradoriids. The non-skeletal phosphatic grains of the Gowers Formation include peloids, ooids and intraclasts, and are associated with scattered glauconite grains.

3.1.4. Materials and methods

Two stratigraphic sections of the Gowers Formation have been studied in detail for this study. Section GF1 is the type section of the Gowers Formation and Bronco Stromatolith Bed, which is Section 418 of Southgate (1986a) (see Fig. 3-1). It occurs on the north side of a prominent east-west ridge located 6 km south of Thornton Homestead. Grid reference for GF1 is 8191 3676 on “Undilla” 1: 100 000 Topographic Sheet 6658 with UTM coordinates of 19° 33’ 07.2” S, 138° 55’ 16.8” E (AG66). GF1 begins at the base of the Gowers Formation type section and runs north-south, with 0 m being at the contact between the Bronco Stromatolith Bed and the Gowers Formation. The tape length of the section is 79 metres with an average dip of 5°, representing a true thickness of 6.62 metres.

Section GF2 is Section 412 of Southgate (1986a). Grid reference is 8196 3596 on the “Undilla” 1: 100 000 sheet with UTM coordinates of 19° 33’ 33.2” S, 138° 55’ 18.2” E (AG66). It begins at the base of the Bronco Stromatolith Bed at 0 m and runs north-south. It has a tape length of 24 metres with a true thickness of 1.99 metres.

Both sections were measured, logged and sampled in detail by Drs J. Paterson and G. Brock (Macquarie University) in 2002. The stratigraphical level of each sample was recorded to within 10 cm and the lithology noted (see Lithology Section).

Examined specimens were mechanically prepared using a vibro tool, coated with black Indian ink, then coated with ammonium chloride to increase the contrast before being photographed. Specimens were photographed using a Canon EOS 5D digital camera with 50 mm and 65 mm objective lenses. Approximately 3000 trilobite and agnostid specimens were examined.

The photographed trilobites and agnostids will be registered and housed at Geoscience Australia, Canberra, Australia.

3.1.5. Local palaeogeography and palaeoenvironment of the Gowers Formation

The sequence stratigraphy and phosphatisation processes documented for the Georgina Basin during Cambrian Series 3, record events which provide a detailed history of the palaeogeography and depositional environments of the region. An epicontinental sea migrated across the Georgina Basin from the south during Ordian time then again in late Templetonian to *A. atavus* time (Shergold and Druce, 1980). This transgression created embayments suitable for the accumulation of organic matter and the precipitation of phosphate. These transgressive pulses led to the deposition of large quantities of organic matter, especially in shallow water environments. The Georgina Basin appears to have been a restricted basin which remained connected to the palaeo-Pacific ocean while sea levels were high.

3.1.6. Sequence Stratigraphy of the Gowers Formation

Sequence stratigraphic analyses of the southern Georgina Basin were conducted in the 1980s in an attempt to gain a better understanding of the prevalent phosphatisation within the region. After revision of the Australian biostratigraphic scheme by Shergold (1989), when the Ordian/Early Templetonian and Late Templetonian/Floran Stages were recognized (refer Fig. 1-3 in Ch. 1), Shergold and Southgate (1988) and Shergold *et al.* (1988) recognised three distinct middle Cambrian phosphogenetic events. A later sequence analysis by Southgate and Shergold (1991) recognized only two major depositional sequences – an Ordian Sequence 1 equivalent to the previous Event 1, and Sequence 2 (late Ordian–early Mindyallan) embracing Events 2 and 3 of Shergold *et al.* (1988), including the Gowers Formation, which was then recognized as *E. opimus* Zone in age. This interpretation of the sequence stratigraphy of the Georgina Basin remains valid (Dunster *et al.*, 2007). The Ordian Sequence 1, characterized by the trilobites *Redlichia* and *Xystridura*, is designated as a Lowstand Systems Tract (LST), while Sequence 2, determined as *T. gibbus* to *A. atavus* in age, represents a Transgressive Systems Tract (TST). The transgressive cycles are thin and poorly developed, suggesting a rapid rise in relative sea level (Southgate and Shergold, 1991).

A eustatic transgressive event has been recognized around the world for the late *T. gibbus* – *A. atavus* interval (Shergold and Druce, 1980; Southgate, 1986b, 1988; Southgate and Shergold, 1991; Ambrose *et al.*, 2001; Howley *et al.*, 2006; Ambrose and Putnam, 2007; Haq and Schutter, 2008; Henderson and Dann, 2010; Gozalo *et al.*, 2011; Peng *et al.*, 2012).

3.1.7. Phosphatisation in the Gowers Formation

Considerable research has been conducted on southern Georgina Basin sediments (Cook and Shergold, 1984, 1986; Southgate, 1983, 1986b; Cook and McElhinny, 1979; Creveling *et al.*, 2014), which contain most of Australia's phosphate reserves, in attempts to shed light on the

process of phosphogenesis. Work by Southgate (1983, 1986b), Cook and Shergold (1986), Shergold and Southgate (1986), Shergold *et al.* (1988), Southgate and Shergold (1991) and Dunster *et al.* (2007), determined the importance of the palaeotopography in relation to phosphatisation. Embayed environments were found to be conducive to the accumulation of organic matter which increased after a transgressive pulse. Most recently, Creveling *et al.* (2014) found that the Cambrian sediments within the southern Georgina Basin accumulated under anoxic, ferruginous conditions, based on data from the Thornton Limestone and Arthur Creek Formation. The Bronco Stromatolith Bed lies unconformably beneath the Gowers Formation and caps the Thornton Limestone, and the lower part of the Arthur Creek Formation appears to be coeval with the Gowers Formation. Southgate (1983) determined the phosphatic lithofacies of the Gowers Formation to be the same as those of the Thornton Limestone. The findings of Creveling *et al.* (2014) are consistent with previous research documenting the propensity for anoxic, ferruginous conditions in late Neoproterozoic and Cambrian oceans (Canfield *et al.*, 2008).

3.1.8. Environmental interpretation of the Gowers Formation

The sedimentary characteristics of the Gowers Formation are typical of a near-shore environment. The phosphatic mudstones and wackestones accumulated in shallow, quiet water, protected (possibly lagoonal) environment. Southgate (1983) interpreted the Gowers Formation as a shallow water lagoon. Ambrose and Putnam (2007) translate the Lower Arthur Creek Formation, a correlative of the Gowers Formation, as anoxic, organic-rich and deposited as apelagic/hemipelagic sediment on an outer ramp. As bacterial degradation of large quantities of organic matter leads to anoxic conditions, it is likely that the Gowers Formation environment became anoxic also.

The Gowers Formation was part of a group of Georgina Basin sites (Hally and Paterson, 2014) found to be closely related (by statistical analysis) and containing many common trilobite genera such as *Asthenopsis*, *Chondranomocare*, *Fuchouia* and *Penarosa* as well as a range of agnostids such as *Acadagnostus*, *Goniagnostus*, *Hypagnostus* and *Rhodotypiscus*. The sites are all found to be shallow marine, intertidal to subtidal settings.

3.2. Australian Cambrian (Series 3) Biostratigraphy

3.2.1. Previous work

Whitehouse (1936) reviewed the geology of Cambrian rocks in the Queensland portion of the Georgina Basin and in 1940 published the first geological maps of Cambrian and Ordovician rocks in Australia. Whitehouse (1927) and Chapman (1929) identified the contained fossils as Middle Cambrian in age – now Cambrian Series 3. Whitehouse (1936, 1939, 1940, 1945) described fossils and added further Cambrian Series 3 localities, demonstrating the wide distribution of these rocks and faunas in the Georgina Basin. In the absence of a stratigraphical sequence, Whitehouse constructed a scale of regional stages based on the occurrences of trilobite and agnostid genera, with two resulting subdivisions – a Templeton Series and Georgina Series. The Templeton Series was intended for the *Redlichia* - *Xystridura* trilobite fauna with the Georgina Series overlying it. A lithological distinction was made, the Templeton Series being comprised of shales and cherts while the Georgina Series was predominantly calcareous. This concept of the Georgina Basin proved to be far too broad and was not followed by Öpik (1957) and subsequent authors. Öpik (1960) originally proposed 12 stages for the Cambrian region of the northwestern area of the Georgina Basin based on trilobite and agnostid ranges. In Öpik and Pritchard's (1960, fig. 14) correlation chart of units in northwest Queensland, the basal Currant Bush Limestone (=

Gowers Formation) of the Undilla Basin is shown as ranging from the upper *T. gibbus* Zone to the *A. atavus* Zone, yet Öpik(1979) classifies this unit as *E. opimus* Zone.

The current northern Australian trilobite and agnostid biozonation for Cambrian Series 3 was initially developed by Öpik (1960, 1961, 1967, 1979). Öpik's scheme was based on spot locality sampling of surface outcrop mainly from the Queensland section of the Georgina Basin. The first scheme was based on Westergård's (1946) classic work which mostly used cosmopolitan agnostids to construct biozones for Cambrian Series 3. Öpik (1960) extended Westergård's (1946) scheme by adding both *gibbus-atavus* and *punctuosus-nathorsti* overlap zones to construct a generalised biostratigraphic scheme. Öpik (1960) retained the *Hypagnostus parvifrons* Zone of Westergård (1946) as "no *Hypagnostus parvifrons* has been found yet in Queensland but a corresponding interval is present in the scale and several species of agnostid await description to complete the scale."

The earlier Ordian and Templetonian stages of Öpik (1956, 1957, 1967, 1970, 1975) proved difficult to subdivide biostratigraphically. Despite the presence in the Templetonian Stage of *T. gibbus* at the top and the *Peronopsis longinqua* Zone (Öpik, 1979) below, neither of which were defined, agnostids were generally scarce so trilobites had to be relied upon for biostratigraphic discrimination. This caused problems especially with *Redlichia* and *Xystridura* as Öpik (1970) had them in reverse stratigraphic order (Kruse *et al.*, 2004). Southgate and Shergold (1991) showed that the

R. chinensis and *X. templetonensis* biofacies were coeval and characteristic of the Ordian Stage. Other *Xystridura*-bearing strata contained agnostids of the *T. gibbus* Zone which led them to question an independent *T. gibbus* Zone. Öpik's (1979) poorly defined *P. longinqua* Zone was considered either coeval with, or predated the *T. gibbus* Zone by Shergold (1989) and led to the pre-*T. gibbus* interval being united with the Ordian stage into one

biostratigraphic unit termed the Ordian/ Early Templetonian Stage with the *T. gibbus* being incorporated with the Floran into a Late Templetonian/Floran Stage. Later, Shergold (1996) revised his interpretation of the *P. longinqua* Zone, believing it to be a lateral equivalent of the *T. gibbus* Zone. Laurie (2006) redefined the Templetonian Stage in Australia to include, in ascending order, the *Pentagnostus anabarensis* Zone, *P. praecurrens* Zone, *P. shergoldi* Zone and *Triplagnostus gibbus* Zone. In redefining the base of Templetonian stage at the FAD of *P. anabarensis*, he established the top of the preceding Stage 5. This led to the current Australian scheme for Cambrian Series 3, consisting of 19 zones grouped into 3 stage-level divisions as shown in Fig. 3 of Chapter 1. This study follows the latest Templetonian revision of Laurie (2006) and revises the current Australian scheme for the *A. atavus* Zone to correspond to the Scandinavian scheme, based on new occurrences of characteristic agnostids in the Gowers Formation (see Figure 3-2).

Southgate and Shergold (1991) recognized that faunas of the Ordian Stage, characterized by *Redlichia chinensis* biofacies, must be coeval with the *Xystridura templetonensis* biofacies which was characteristic of the Beetle Creek Formation. There was a need to discriminate the *X. templetonensis*-containing strata from those which contained *Xystridura* and agnostids of the *T. gibbus* Zone. This led to the concept of the Templetonian stage being divided into lower and upper parts, each being annexed to its adjacent stages to produce an earliest Middle Cambrian Ordian–early Templetonian Stage and a succeeding late Templetonian–Floran Stage (Shergold 1989, 1995). As then understood, this latter stage commenced with the *Triplagnostus gibbus* Zone (Öpik, 1968), the earliest agnostine zone recognised at that time.

The *Acidusus atavus* Zone is well defined throughout the world, its base marked by the FAD of *A. atavus*. Westergård's (1946) scheme divided what is now the *A. atavus* Zone into a lower *Tomagnostus fissus* - *A. atavus* subzone and an upper *Hypagnostus parvifrons* subzone

(see Peng and Robison, 2000, fig. 2; Weidner and Nielsen, 2013, Fig. 2). Westergård (1946) found that *H. parvifrons* first appeared in the lower *atavus* Zone but became more abundant in the upper *atavus* Zone, apparently due to local taxon abundance (Berg-Madsen, 1985). Some studies have reported the first appearances of *A. atavus* and *H. parvifrons* at close stratigraphic levels in China, Siberia and the United States (Peng and Robison, 2000). However, *A. atavus* has a short stratigraphic range while *H. parvifrons* has a much longer range, making *A. atavus* more useful as a biostratigraphic indicator.

Öpik (1979) introduced the Floran Stage into the Australian scheme, where he replaced the *H. parvifrons* Zone of Westergård with the *E. opimus* Zone due to the rarity of *H. parvifrons* in the Georgina Basin. *Euagnostus opimus* was originally named by Whitehouse (1936), who illustrated only one cephalon and two pygidia. Robison (*in* Jell and Robison, 1978) reviewed Whitehouse's types and reassigned the holotype pygidium of *E. opimus* to *Peronopsis*, a paratype pygidium to *Baltagnostus*, and the paratype cephalon to *Doryagnostus*. *Euagnostus opimus* closely resembles *E. interstrictus* (White, 1874), differing mainly in the depth of the preglabellar furrow. However, as the preglabellar furrow varies in depth in this species (Robison *in* Jell and Robison, 1978, pl. 2, figs. 1–3), *E. opimus* may be a geographic variant of *E. interstrictus* (Peng and Robison, 2000). *E. interstrictus* in North America ranges from the upper *Triplagnostus gibbus* Zone to the upper *Ptychagnostus punctuosus* Zone. Given that Öpik (1979) replaced the name “*H. parvifrons*” due only to the rarity of *H. parvifrons* in Australia, combined with the doubt over the designation of *E. opimus* specimens, it seems appropriate here, with the discovery of *H. parvifrons* specimens in the lower *A. atavus* Zone in the Gowers Formation, to replace the scheme of Öpik (1979) with one which correlates with the modern Scandinavian scheme of Høyberget and Bruton (2008) and Weidner and Nielsen (2009; 2013) as shown in Figure 3-2. Mens *et al.* (1990) suppressed

the *H. parvifrons* Zone referring strata to the *P. atavus* Zone but considered that it may be useful to recognize the zone in some local situations.

3.2.2. Biostratigraphy

Õpik (1979; 1982), Jell and Robison (1978) and Jell (1978) published comprehensive taxonomic works on many of the trilobites and agnostids from the Gowers Formation (referred to therein as the Currant Bush Limestone), but, until now, a detailed biostratigraphical analysis of these arthropod faunas from the Gowers Formation has not been undertaken. The detailed sampling undertaken for this study, together with the earlier works mentioned above and recent work by Laurie (2004, 2006, 2012, 2014) on the Arthur Creek Formation of the Georgina Basin, Sun *et al.* (2013) on the Warburton Basin and Smith *et al.* (2015) on the Amadeus Basin, has produced a much more comprehensive understanding of the stratigraphical distribution of Cambrian Series 3 trilobite and agnostid species from Australia.

Lenz *et al.* (1993) called for a clear distinction between the definition and characterization of all biozones. The names of the biozones facilitate communication and the eponymous species need neither be confined to that zone nor everywhere have the same stratigraphic range. Each zone of Cambrian Series 3 from *T. gibbus* to *Lejopyge laevigata*, can be characterised by an assemblage of agnostoid species. This study details characteristic assemblages from the *T. gibbus* Zone to the lower *A. atavus* Zone of the Gowers Formation. The *T. gibbus* Zone is recognized by a typical *T. gibbus*-type assemblage consisting of the agnostids *Rhodotypiscus nasonis*, *Euagnostus interstrictus*, *Goniagnostus lemniscatus*, *Onymagnostus semiermis* and *Peronopsis amplaxis*; however, the lower section of GF1 of the Gowers Formation does not contain *T. gibbus* specimens. In the Great Basin of the US, the incoming *gibbus* fauna is associated with a marked regional change in lithofacies and the inferred depositional

environment (Robison, 1984). Robison (1984) states that comparable situations occur elsewhere, where the lower beds of *gibbus* Zone age rest on shallow-water facies. In the absence of Templetonian *Pentagnostus* species, precise correlation is not possible for the base of the *T. gibbus* Zone in the Gowers Formation.

Unlike the base of the *T.gibbus* Zone, the base of the *A. atavus* Zone is easily recognized around the world. In the Gowers Formation, the first appearance of *H. parvifrons*, which is confined to the *A. atavus* Zone on all other continents, most probably marks the base of the *A. atavus* Zone as it also coincides with the appearance of the trilobites *Chondranomocare confertum* and *Penarosa retifera* which are elsewhere in Australia confined to the *atavus* Zone. Also, the appearance of *H. parvifrons* in the Gowers Formation coincides with the last appearance of *Peronopsis amplaxis* which is confined to the *T. gibbus* Zone in the U.S. (Robison, 1982, 1984). *Euagnostus interstrictus*, *Onymagnostus semiermis*, and *Acadagnostus rakuroensis* continue into the *A. atavus* Zone. The Gowers Formation does demonstrate a change in lithology prior to the entry of *H. parvifrons*, from predominantly mudstones with minor limestones to wackestones. This change in constituent species together with a change in lithology may also signify the DICE event associated with the beginning of the *A. atavus* Zone elsewhere in the world.

		Australia		Scandinavia		North America		South China		
		This paper		Westergård (1946)	Weidner & Nielsen (2009, 2013)					
Cambrian Series 3	Drumian	Undillan	<i>Goniagnostus nathorsti</i>	<i>Ptychagnostus punctuosus</i>	<i>G. nathorsti</i>	Marjuman	<i>Ptychagnostus punctuosus</i>	Wangcunian	<i>G. nathorsti</i>	
			<i>Doryagnostus deltooides</i>		<i>Ptychagnostus punctuosus</i>					
		Floran	upper <i>Acidusus atavus</i>	<i>Hypagnostus parvifrons</i>	upper <i>Acidusus atavus</i>				<i>Ptychagnostus atavus</i>	<i>A. atavus</i>
			lower <i>Ptychagnostus atavus</i>	<i>Tomagnostus fissus</i> <i>-Ptychagnostus atavus</i>	lower					
	Stage 5	Templetonian	<i>Triplagnostus gibbus</i>	<i>Ptychagnostus gibbus</i>	<i>Triplagnostus gibbus</i>	Togazhan	<i>Ptychagnostus gibbus</i>	Tajjiangian	<i>Ptychagnostus gibbus</i>	
			<i>Pentagnostus shergoldi</i>		<i>Paradoxides pinus</i>	Delamaran	<i>Pentagnostus praecurrens</i>		<i>Peronopsis tajjianensis</i>	
			<i>P. praecurrens</i>		? ? ? ?		<i>Oryctocephalus indicus</i>		<i>Oryctocephalus indicus</i>	
		<i>P. anabarensis</i>		<i>P. insularis</i>						
			<i>P. krusei</i>							

Figure 3-2. International Correlation of Cambrian Series 3 for Australia, North America, Scandinavia and South China. Stages and zones from Peng et al. (2012).

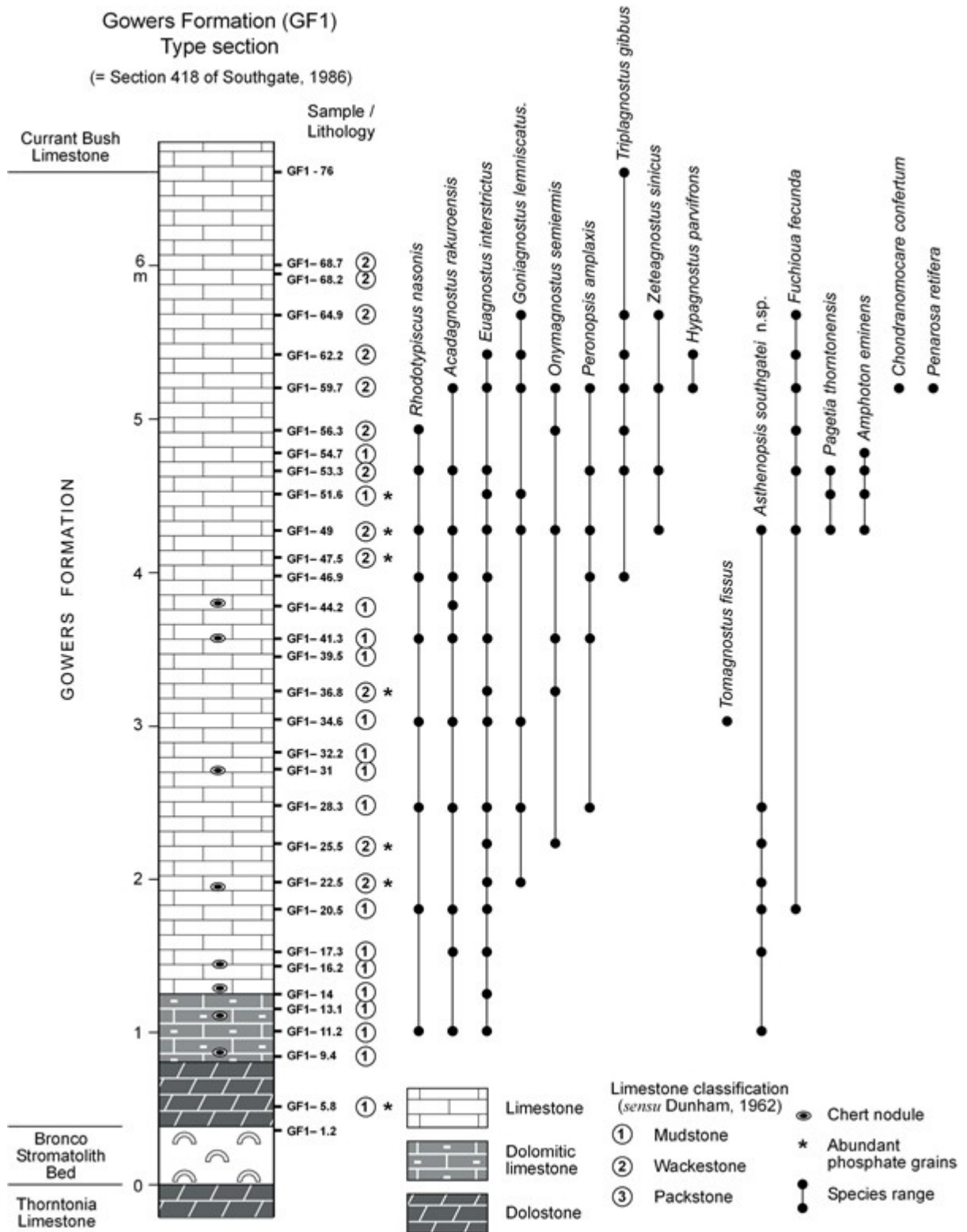


Figure 3-3 Range Chart for all species in section GF1 of the Gowers Formation.

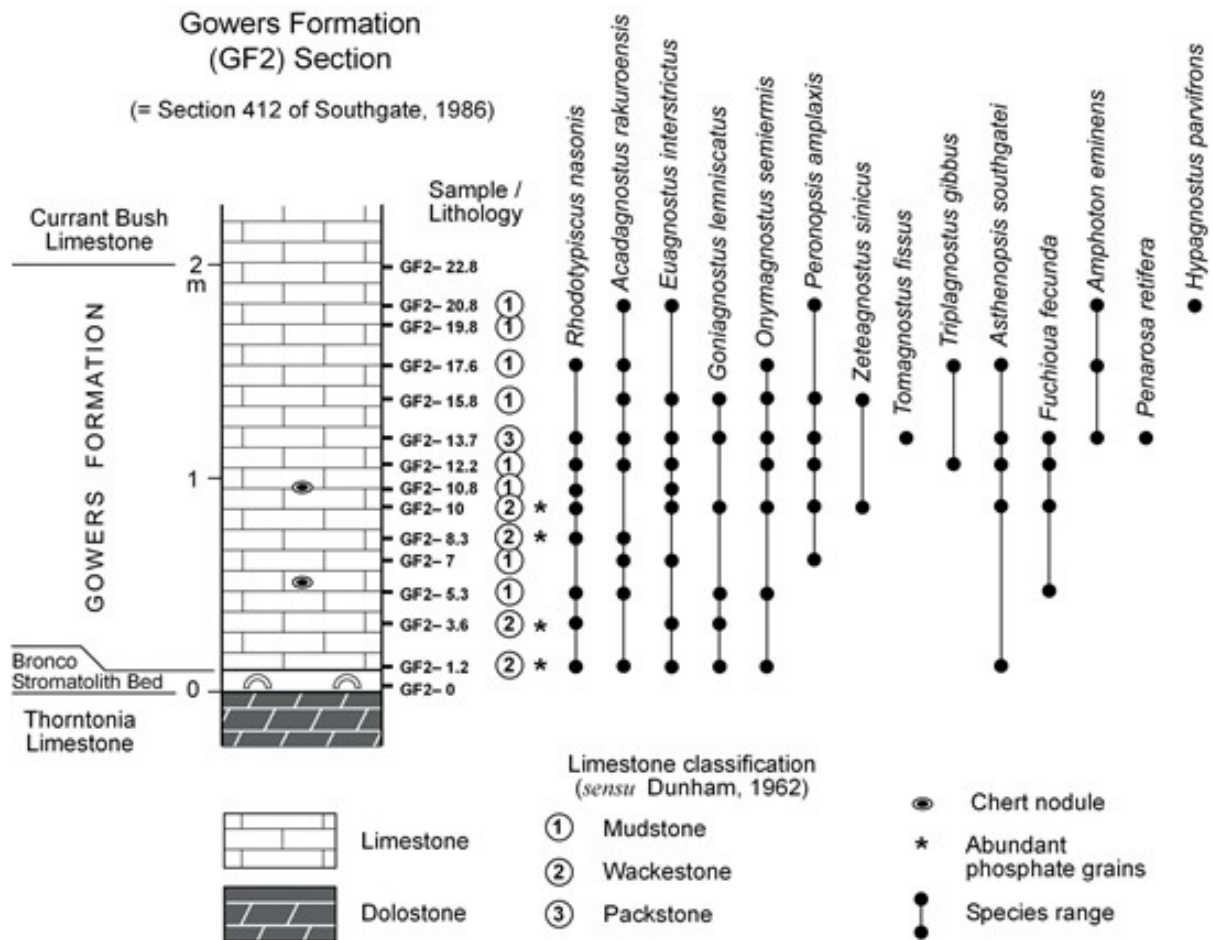


Figure 3-4. Range Chart for all species in section GF2 of the Gowers Formation.

3.3. The age of the Gowers Formation: new biostratigraphic data

Section GF1 material has been divided into three intervals based on the biostratigraphic range of taxa: 1) sampled horizons 11.2 to 46.9, the pre- *T. gibbus* section, -2) horizons 46.9 to 59.7, where *H. parvifrons* first appears, and 3) horizons 59.7 to 76, the upper section after FAD of *H. parvifrons*.

Interval 1. Horizons GF1: 11.2 to 46.9: This interval contains *Acadagnostus rakuroensis* (Kobayashi 1939), *Asthenopsis southgatei* n. sp., *Euagnostus interstrictus* (White 1874), *Onymagnostus semiermis* Öpik, 1979, *Peronopsis amplaxis* Robison, 1982, *Goniagnostus*

lemniscatus Öpik, 1979, *Rhodotypiscus nasonis* Öpik, 1979 and *Fuchouia fecunda* Öpik, 1982. *Triplagnostus gibbus* first appears at 46.9 m.

Of these species, only *P. amplaxis* from Utah (Robison, 1982, 1984) is useful for correlation as it is confined to the *T. gibbus* Zone, while all other species have a longer range, and one is a new species. However, the co-occurrence of these species with *T. gibbus* in other parts of the world confirms their assignment to the *T. gibbus* Zone (Robison, 1982; Westrop *et al.*, 1996; Weidner and Nielsen, 2013).

Acadagnostus rakuroensis is recorded from the basal Middle Cambrian Mapan Formation in China (Zhang and Jell, 1987). This species is known in Australia from the Currant Bush Limestone (Jell and Robison, 1978) and the Arthur Creek Formation (Laurie, 2014) in rocks dated as Templetonian to *E. opimus* Zone. Specimens from China (Walcott, 1911; Resser and Endo, 1937; Kobayashi, 1962; Chang in Lu *et al.*, 1965), ?North Korea (Kobayashi, 1962) and Russia (Ivshin, 1953) have not been dated more specifically than basal Middle Cambrian. Its taxonomic history is somewhat complicated and is discussed in the Systematics section.

Euagnostus aff. *interstrictus* is found in the lower *A. atavus* Zone of Sweden (Weidner and Nielsen, 2013), in the *Pentagnostus shergoldi* and *P. praecurrens* Zones in the Arthur Creek Formation of the western Georgina Basin (Laurie, 2004, 2006) and possibly in the Scarr 1 drillhole in the central Georgina Basin (Laurie, 2014), which is perhaps *A. atavus* Zone in age. Laurie (2004) considered *E. aff. interstrictus* to be a separate species from *E. interstrictus* based on several traits which are herein found to be intraspecific variables. *Euagnostus interstrictus* (*sensu stricto*) occurs in the *T. gibbus* to *P. punctuosus* Zones in Utah and Nevada (Young and Ludvigsen, 1989). In the GF1 section, it ranges from the *T. gibbus* Zone to the lower *A. atavus* Zone.

Rhodotyphiscus nasonis was found to be a common species in the Currant Bush Limestone by Öpik (1979)—including a locality that would now represent the Gowers Formation—as well as in the Inca and Age Creek Formations of the Georgina Basin. Öpik (1979) determined these localities to be *E. opimus* Zone in age. It is found to be a long-ranging species in the Gowers Formation, ranging from horizons 11.7 to 53.3 in GF1 and 1.2 to 17.6 in GF2, spanning the *T. gibbus* to lower *A. atavus* interval. The species is documented from Reilly Ridge, Antarctica (Jago and Cooper, 2007) as *A. atavus* to *E. opimus* in age, partly based on Öpik's questionable *E. opimus* date for the Currant Bush Limestone.

Onymagnostus semiermis ranges from horizons 28.3 to 59.7 in GF1 and from 1.2 to 17.6 in GF2. Öpik (1979) found specimens in the Currant Bush Limestone at a locality most likely to represent the Gowers Formation. The species is also found in the *E. opimus* Zone of the Inca Formation in the Georgina Basin. Laurie (2014) tentatively assigned a cephalon from the Scarr 1 Drillhole in the Georgina Basin to *Onymagnostus*, stating that it came from early in the range of the genus due to its arcuate scrobicules, and considers this may be the *E. opimus* Zone. It is most likely *O. semiermis* rather than another species of *Onymagnostus* due to its arcuate scrobicules. Laurie (2006) also found this species in the Arthur Creek Formation in the Georgina Basin above the *P. shergoldi* Zone, making it a correlative of the Gowers Formation. The Scarr drillhole contains a specimen assigned to? *Onymagnostus* which has arcuate scrobicules, similar to those of *O. semiermis* specimens from the Gowers Formation. If, as Laurie (2014) states, this indicates that the specimen comes from early in the range of the genus, then this could indicate a *gibbus* or *atavus* Zone age for the Scarr fauna rather than the *E. opimus* age he assigns it.

Goniagnostus lemniscatus ranges from horizons 22.5 to 64.9 in section GF1 and 1.2 to 15.8 in section GF2. Laurie (1989) states that the genus is found in the *A. atavus* and *E. opimus*

Zones only and that earlier species have well-developed arcuate scrobicules. The arcuate scrobicules are an ontogenetic feature of *G. lemniscatus*, appearing when the cephalon reaches about 2 mm in length, about half their adult length. Larger specimens from the Gowers all demonstrate arcuate scrobicules and are found at the lowest levels in the GF1 section in the *T. gibbus* Zone. They therefore extend the lower range for this species and the genus. The *Criotypus* specimens from the Scarr drillhole (Laurie 2014, Fig. 3A, E, F, I) are juvenile *G. lemniscatus*.

Tomagnostus fissus is found in Australia for the first time in this study. *T. fissus* is a very widespread species reported from Sweden (Westergård, 1946; Weidner & Nielsen, 2013), Norway (Høyberget and Bruton, 2008), Great Britain (Thomas *et al.*, 1984; Bridge *et al.*, 1998), eastern Canada (Hutchinson, 1962; Kindle, 1982), U.S.A. (Samson *et al.*, 1990), Greenland (Robison, 1994) and Siberia (Egorova *et al.*, 1982). It is known from the *T. gibbus* and *A. atavus* Zones in Sweden, Denmark, Greenland, England, Wales, Canada, U.S.A. and Russia, and the *A. atavus* Zone in Norway. It is known from shallow- to deep-water lithofacies of high palaeolatitudes but from only deep-water lithofacies of low palaeolatitudes (Peng and Robison, 2000). In the Gowers Formation, despite the paucity of cephalons, *T. fissus* is readily distinguished from other agnostids including congeners (Weidner and Nielsen, 2013).

Fuchouia fecunda was considered to be *E. opimus* Zone in age by Öpik (1982) due to it being found in the Currant Bush Limestone, but as previously mentioned, this date is questionable. Laurie (2006) described specimens from the Templetonian part of the Arthur Creek Formation of the Georgina Basin, which are probably *T. gibbus* Zone in age.

Interval 2. Horizons GF1: 46.9 to 59.7: *Amphoton eminens* Öpik, *Pagetia thurstonensis* Jell, *Acadagnostus rakuroensis* Kobayashi, *Rhodotypiscus nasonis* Öpik, *Euagnostus*

interstrictus White, *Goniagnostus lemniscatus* Öpik, *Peronopsis amplaxis* Robison, *Triplagnostus gibbus* Linnarsson and *Zeteagnostus sinicus* Lu.

Triplagnostus gibbus first appears in GF1 at horizon 46.9 and in GF2 at horizon 12.2. in both Sweden (Ahlberg *et al.*, 2007) and the United States (Robison, 1984), the base of the *T. gibbus* Zone is defined by the FAD of the eponymous species and the species ranges globally into the lower *A. atavus* Zone. However, the base of the *T. gibbus* Zone may not represent a precise time horizon due to the fact that the FAD of *T. gibbus* at some localities is in strata directly overlying a significant erosional contact (Babcock *et al.*, 2007). In the Great Basin of the United States, the incoming *T. gibbus* fauna is associated with a marked regional change in lithofacies (Robison, 1984; Rowell *et al.*, 1982). Hence this part of GF1, from 46.9 to 59.7, with the presence of *P. amplaxis* and the co-occurrence of *Rhodotypiscus nasonis*, *Onymagnostus semiermis*, *Goniagnostus lemniscatus* and *Euagnostus interstrictus*, is most likely upper *T. gibbus* Zone in age.

Interval 3. Horizons GF1: 59.7 to 76: *Hypagnostus parvifrons* (Linnarsson) , *Zeteagnostus sinicus* Lu, *Penarosa retifera* Öpik, *Chondranomocare confertum* Whitehouse, *T. gibbus* Linnarsson, *Goniagnostus lemniscatus* Öpik, *Euagnostus interstrictus* White and *Fuchouia fecunda* Öpik.

The base of the Floran Stage was defined by Öpik (1979) as comprising a lower *A. atavus* Zone and an upper *E. opimus* Zone. Öpik did not formally define the *A. atavus* Zone, but regarded the eponymous species as being confined to that zone (Öpik 1979, table 1). Öpik's understanding of the definition of the *A. atavus* Zone is unclear as he placed FAD of *Acidusus atavus* above the base of Floran (Öpik, 1979, table 2) (Laurie, 2006). Westergård (1946) similarly, did not define the base of the *A. atavus* Zone (Axheimer and Ahlberg, 2003). Laurie (2006) defined base of the *A. atavus* Zone in Australia at the FAD of the eponymous

species. This species does not appear in the Gowers Formation, making the lower boundary of the *atavus* Zone more difficult to pinpoint. However, *H. parvifrons* is found in the Gowers Formation, with Öpik (1979) having previously recorded only one specimen in Australia. *Hypagnostus parvifrons* is a very widespread species around the world, being restricted to the *A. atavus* and *P. punctuosus* Zones in Laurentia (Samson *et al.*, 1990; Robison 1984), Sweden (Weidner and Nielsen, 2013), western Newfoundland (Westrop *et al.*, 1996), Argentina (Tortello and Bordonaro, 1997), Norway (Høyberget and Bruton, 2008) and North Greenland (Robison, 1994). In Hunan, *Hypagnostus parvifrons* extends from the base of the *Ptychagnostus atavus* Zone and into the *Linguagnostus reconditus* Zone (Peng & Robison, 2000). Thus, the first appearances of *A. atavus* and *H. parvifrons* occur at close stratigraphic levels in widely separated regions of the world (China, Siberia, United States), suggesting that horizon GF1-59.7 could represent an approximate boundary for the base the *A. atavus* Zone in the Gowers Formation. The fact that *P. amplaxis* disappears at GF1-59.7 and *T. gibbus* continues, supports the fact that this part of GF1 is of lower *A. atavus* Zone age. *Zeteagnostus sinicus* is elsewhere dated as *T. gibbus* to lower *A. atavus* Zone (Ahlberg *et al.*, 2007).

Hypagnostus parvifrons is found in the Gowers Formation in GF1 at levels 59.7 and 62.2 and in GF2 at level 20.8. An obvious faunal change occurs in GF1 from 53.3 to 59.7 where *H. parvifrons*, *C. confertum* and *P. retifera* appear and *R. nasonis*, *A. southgatei*, *O. semiermis*, *P. amplaxis*, *P. thurstonensis* and *A. eminens* disappear. A similar change occurs in Section GF2 at level 17.6 where *R. nasonis*, *O. semiermis*, *T. gibbus* and disappear.

Triplagnostus gibbus continues in GF1 until horizon 76, into the lower *A. atavus* Zone, which is a reoccurring pattern around the world (Weidner and Nielsen, 2013). In the Warburton Basin of South Australia, *Fuchouia fecunda* ranges from *T. gibbus* to *E. opimus* zones (Jago

et. al., 2006) and in the Arthur Creek Formation, Georgina Basin, it is found high in the Templetonian or slightly above (Laurie, 2006). It is also found in the *A. atavus* part of the Age Creek and Inca Formations (Öpik, 1979).

3.4. Systematic Palaeontology

Classification

It is herein recognized that trilobites and agnostids are two separate arthropod groups (Adrain, 2011; Hally and Paterson, 2014). Agnostid classification follows Shergold and Laurie (1997), and the suprageneric classification of trilobites follows Fortey (1997).

Terminology

Agnostoid terminology used herein is based mainly on that of Öpik (1961, 1967, 1979), except for the notation of intra-axial furrows (F1, F2, F3) and pygidial axial lobes (M1, M2, posteroaxis), which were defined by Robison (1982, p. 134) and used by Laurie (1988, 2004, 2006). Laurie (1988, p. 171) defined other terms for the shape of the posterior glabellar lobe. The articulating half-ring is included as part of the pygidial axis (*sensu* Laurie, 2006).

Class uncertain

Order AGNOSTIDA Salter, 1864

Superfamily AGNOSTOIDEA McCoy, 1849

Family AGNOSTIDAE McCoy, 1849

Subfamily AGNOSTINAE McCoy, 1849

Family PTYCHAGNOSTIDAE Kobayashi, 1939

Goniagnostus Howell 1935a

Type species. *Agnostus nathorsti* Brögger 1878.

Diagnosis. See Peng & Robison (2000, p. 71).

Remarks. Öpik (1979) described 10 Cambrian Series 3 species of *Goniagnostus* in three subgenera, *G. (Goniagnostus)*, *G. (Criotypus)* and *G. (Allbodochus)*. The subgenera are based on the presence or absence of paired arcuate scrobicules, differences in attenuation of the posteroaxis and the depth of the transverse sulcus. I follow Peng & Robison (2000) in regarding these to be specific character traits rather than subgeneric and herein refer to the Gowers species as *Goniagnostus lemniscatus* Öpik, 1979. Australian specimens of *G. lemniscatus* from the Georgina Basin have well developed arcuate scrobicules (Laurie, 1989). The Gowers specimens show well developed arcuate scrobicules on reaching maturity, which occurs when the cephalon reaches about 3.5mm in length.

3.4.1. *Goniagnostus lemniscatus* Öpik 1979 (Fig. 3-5A-P, 3-6A-P)

1979 *Goniagnostus (Criotypus) lemniscatus* Öpik, p. 147, pl. 58, figs 1-8; pl. 59, fig. 1.

1979 *Goniagnostus (Criotypus)* sp. nov. aff. *lemniscatus* Öpik, p. 149, pl. 59, figs 2, 3.

1979 *Goniagnostus (Criotypus) paenerugatus* Öpik, p. 149, pl. 45, fig. 5; pl. 59, figs 4-6.

2006? *Goniagnostus (Criotypus)* sp., Laurie, Fig. 14.

Material. CPC XXGLa-XXGLm, four complete specimens, 12 cephalata, 16 pygidia from GF1: 22.5–64.9, GF2: 1.2–15.8; *T. gibbus* to *A. atavus* Zones.

Emended diagnosis. Exoskeleton large, cephalic spines absent. Thorax with axial spine but lacking fulcral spines on posterior segment. Cephalon with well- developed arcuate scrobicules and accompanying radial scrobicules around anterior margin. Pygidium with short marginal spine and distinctive secondary node.

Description. Large agnostid, reaching 10-11mm length in maturity. Cephalon semi- elliptical in outline, length 90–96 % of width (n =10), nonspinose; moderately convex; glabella flanked by a pair of arcuate scrobicules which sometimes vary in shape and only develop after the cephalon reaches a mature size of about 3.5 mm in cephalic length; radial scrobicules around margin, generally becoming longer towards posterior but to no exact pattern; border narrow, roll-like, border furrow well developed and very narrow; preglabellar median furrow well defined; sulcus about 30% of anteroglabellar length, undefined in juvenile specimens; usually well-defined glabella 69–90% (n =12) of cephalic length, 64% in very small specimen; anterior lobe well developed, occupying 29–34% (n =13) of glabellar length, triangular (equilateral) in shape; F3 straight to slightly curved posteriorly, often incised more deeply on lateral edges of glabella; posterior glabellar lobe increasing slightly in width, culmination rising high and narrow, being compressed laterally; occipital spine behind this culmination being a retral spike; F2 furrows well developed; F1 undeveloped; apodemal pits at the adaxial front of basal lobes; basal lobes large, tumid and divided into a narrow anterior which reaches the apodemal pits and a wider posterior boss.

Thorax nonspinose, with elements well defined; anterior segment with well developed pleural furrows separating a triangular posterior pleural band from a bulbous anterior pleural band; clearly developed lateral lobes and broad (tr.) trapeziform median lobe; posterior segment with well developed pleural furrows separating narrow anterior pleural band from laterally

tapering posterior pleural band; axial lobe with well defined lateral lobes and broad arcuate median lobe.

Pygidium subquadrate in outline, length: width = 80–97% (n = 12), moderately convex, with short posterolateral spines; border of moderate width, slightly flattened, border furrow varies morphologically from narrow to wide; postaxial median furrow not well defined but usually present; axis 73–83% as long, 32–40% as wide (n = 15), increasing in width with maturity, posteriorly bluntly pointed or narrowly rounded, moderately convex; large prominent axial node; F1 well defined, bent strongly forward; M1 broad (tr.), lateral margins convex; F2 bent posteriorly around prominent median node, well defined; M2 constricted, with margins weakly convex; posteroaxis ogival, occupying 41–68 % (n = 13) of axial length which increases with maturity, with maximum width about midlength; small secondary node always present, at or very slightly behind lobe midlength. Postaxial median furrow present in juveniles, becoming shorter or non-existent in adults.

Remarks. Öpik's (1979) specimens found at Locality M150 in the Currant Bush Limestone, very close to the Gowers Formation type section, may have derived from the latter unit. This species of *Goniagnostus* possesses arcuate scrobicules unlike other species in the genus. The abundant specimens found in the Gowers Formation show that scrobicules become better developed throughout ontogeny, with juvenile specimens such as those illustrated in Figs 3-6N, 3-6O and 3-6P, displaying relatively weak scrobiculation. It appears that the arcuate scrobicules develop after the lateral scrobicules, with the latter becoming better developed with growth. Length: width is smaller in the holotype and paratypes which come from a different locality and found in shale.

Onymagnostus Öpik, 1979

1979 *Onymagnostus* (*Agnostonymus*) Öpik, p. 114.

1984 *Onymagnostus* Öpik, Robison, p. 50.

Type species. *Onymagnostus angulatus* Öpik, 1979, p. 108 [= *O. hybridus*

(Brögger, 1878] OD.

Figure 3-5 *Goniagnostus lemniscatus* **A.** cephalon and pygidium of specimen CPC XXXXX, from GF2, level 12.2, x 8.1; **B.** entire specimen CPC XXXXX, from GF2, level 15.8 - a young specimen with narrow pygidial axis and a postaxial median furrow with the arcuate scrobicules well-developed, x17.5; **C.** entire specimen CPC XXXXX, from GF2, level 12.2 – a young specimen with a narrow pygidial axis and a postaxial median furrow, also with arcuate scrobicules which are less well-developed than in B., x17.4; **D.** latex cast of broken entire specimen CPC XXXXX, from GF2, level 15.8, young specimen with narrow pygidial axis and postaxial median furrow, x13.3; **E – P** are cephalia, **E.** CPC XXXXX, from GF1, level 51.6, x 7.8; **F.** CPC XXXXX, from GF2, level 13.7, x 8.5; **G.** CPC XXXXX, from GF2, level 12.2, x 9.2; **H.** CPC XXXXX, from GF2, level 12.2, x 11.5; **I.** CPC XXXXX, from GF1, level 34.6, x 7.7; **J.** broken specimen CPC XXXXX, from GF2, level 12.2, x 9.3; **K.** CPC XXXXX, from GF2, level 3.6, x 8.9; **L.** broken specimen CPC XXXXX, from GF2, level 12.2, x 8.6; **M.** CPC XXXXX, from GF1, level 59.7, young specimen with less developed cephalic scrobicules and intact cephalic spine, x10.0; **N.** CPC XXXXX, from GF1, level 62.2, young specimen with vague arcuate scrobicules, x10.6; **O.** CPC XXXXX, from GF1, level 64.9, young specimen showing no arcuate scrobicules and undeveloped radial scrobicules, x 10.6; **P.** CPC XXXXX, from GF1, level 64.9, young specimen without arcuate scrobicules and undeveloped straight scrobicules, x11.0.

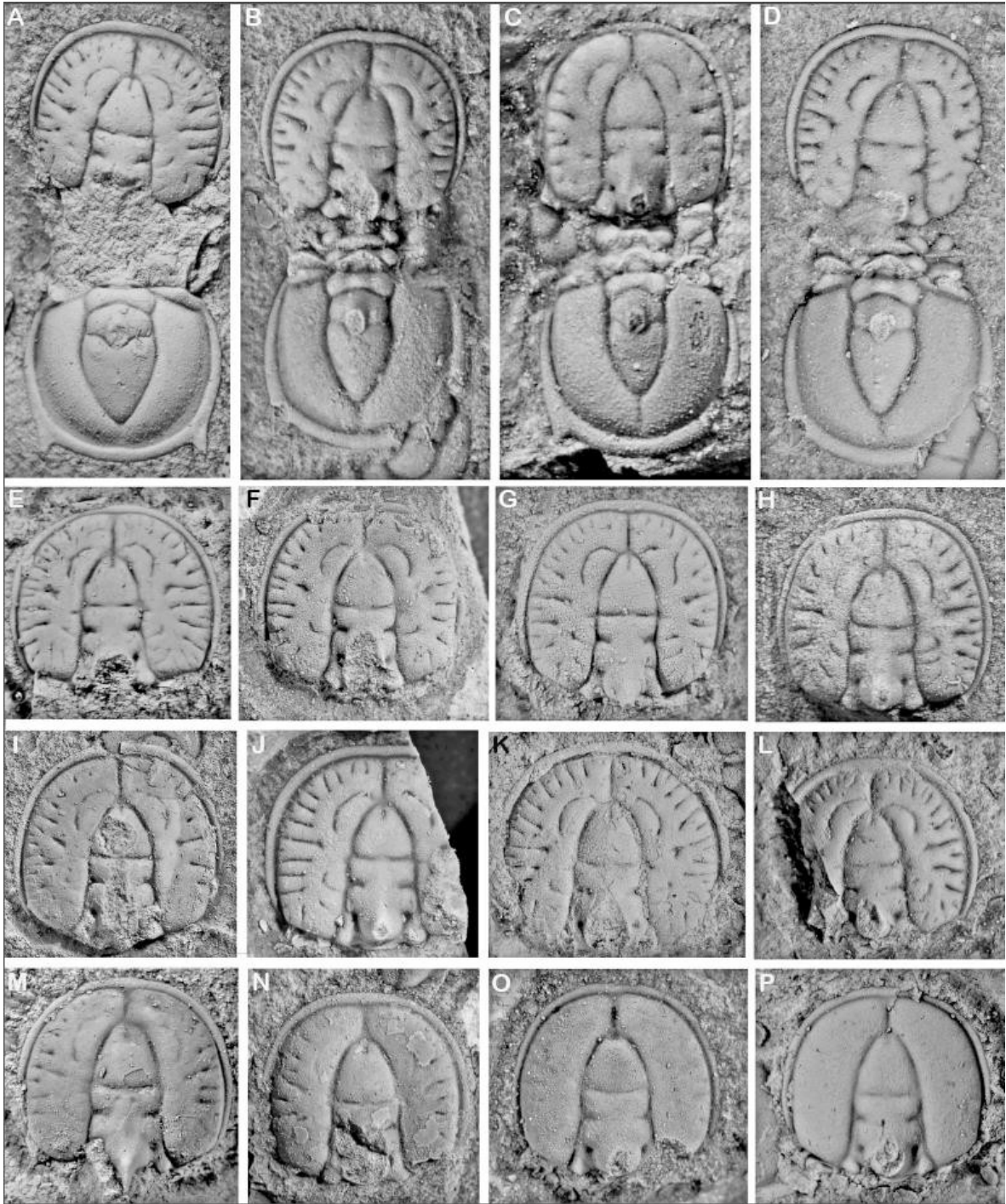


Figure 3-5 *Goniagnostus lemniscatus*

Figure 3-6 *Goniagnostus lemniscatus* pygidia: **A.** CPC XXXXX, from GF2, level 12.2, adult with a postaxial median furrow, x 8.5; **B.** CPC XXXXX, from GF1, level 51.6, no postaxial furrow, a conspicuous secondary node, x 7.9; **C.** CPC XXXXX, from GF2, level 13.7, shallow postaxial furrow, x8.6; **D.** CPC XXXXX, from GF2, level 12.2, very shallow postaxial furrow and conspicuous secondary node, x8.0; **E.** CPC XXXXX, from GF1, level 51.6, postaxial median furrow, x 6.7; **F.** CPC XXXXX, from GF2, level 12.2, with very wide border furrow and rounded axis tip, x 15.9 **G.** CPC XXXXX, from GF2, level 10, with wide border furrow, x7.6; **H.** CPC XXXXX, from GF1, level 49, younger specimen with a narrower axis, well-developed postaxial median furrow and a conspicuous secondary node, 10.5; **I.** CPC XXXXX, from GF1, level 59.7, no postaxial median furrow and conspicuous secondary node, x 8.3; **J.** damaged specimen CPC XXXXX, from GF1, level 59.7, x 9.3; **K.** CPC XXXXX, from GF1, level 59.7, with wide axis, x 9.0; **L.** CPC XXXXX, from GF2, level 12.2, with wide border furrow, x 9.0; **M.** CPC XXXXX, from GF2, level 12.2, x 8.9; **N.** CPC XXXXX, from GF2, level 12.2, x 8.0; **O.** CPC XXXXX, from GF2, level 12.2, with wide axis and a conspicuous secondary node, x 9.2; **P.** CPC XXXXX, from GF2, level 12.2, x 8.3

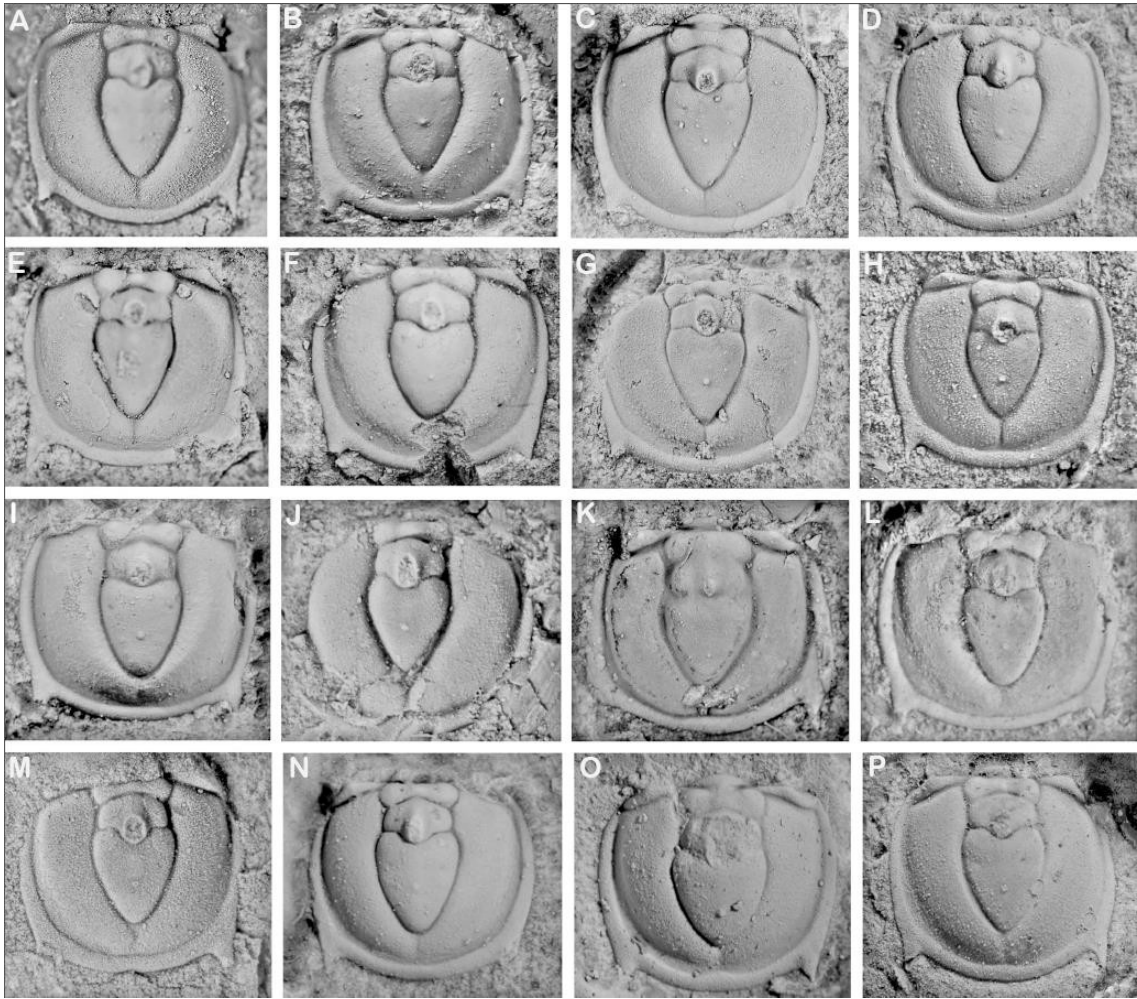


Figure 3-6 *Goniagnostus lemniscatus*

Diagnosis. See Shergold & Laurie (1997, p. 352).

3.4.2. *Onymagnostus semiermis* Öpik, 1979 (Fig. 3-7A-T, Fig. 3-8A-X)

1979 *Onymagnostus (Agnostonymus) semiermis* Öpik, p. 114-115, pl. 54, figs 1-8.

1979 *Onymagnostus* sp. nov. aff. *angulatus* Öpik, p. 110, pl. 51, figs 4, 5.

1988 *Onymagnostus semiermis* Öpik; Laurie, p. 189, fig. 14.

Diagnosis. See Laurie (1988, p. 189)

Material. Pl. XXOSA-T and Pl. XXOS2A-X, four complete specimens, 16 cephalata, 24 pygidia, GF1: 25.5–59.7, GF2: 1.2–17.6; *T. gibbus* Zone.

Description. A moderately large agnostid, attaining a length of at least 11.1 mm (Fig. 3-7A). Cephalon moderately convex, semioval in outline, length 80–97% width (av. = 90%, n = 24), often scrobiculate, with weak arcuate scrobicules and weak short lines of varying length on the cephalic margin; glabella narrow, usually one-third of cephalic width but varying from 28–34% (n = 19); glabellar length 70–86% (n = 18) but usually 74% of cephalic length; border narrow, slightly flattened; border furrow very narrow, moderately deep; preglabellar median furrow moderately narrow and shallow, 13–20% glabellar length (sag.) (av. = 16%, n = 24), sometimes forming a small deltoid area where it meets the anterior glabella (Fig. 3-7G); anterior lobe semioval in shape, rounded to acutely angled anteriorly, occupying 34 to 38% (n = 11) of glabellar length. F3 clearly incised, straight or bowed slightly rearward; posterior glabellar lobe slightly expanded medially, strongly inflated posteriorly, with F2 furrows weakly developed as faint notches indenting lobe margin. F1 furrows weakly developed as indentations about level with anterior extremities of basal lobes; glabellar node

located about halfway along length of posteroaxis; basal lobes small, elongate, with a broad (tr.) bulbous posterior portion and a narrow anterior portion. Cephalon smooth.

Thorax unknown.

Pygidium semioval in outline, length 79–96% of width (n =14), strongly convex, with minute posterolateral spines; border of moderate width, flattened; border furrow narrow to slightly wider; postaxial median furrow usually absent, present in one younger specimen where it is shallow and 13% of pygidial length. Axis usually 34% of pygidial width, 80–86% pygidial length, constricted at F1 furrow, widest across M1 lobe; posterior extremity rounded; F1 strongly deflected forward adaxially; F2 very strongly deflected around large elongate median node; M2 constricted, margins straight to very slightly convex; posteroaxis ogival with maximum width at anterior, one-third of axis length. Secondary node when present, is placed centrally. Pygidium smooth.

Remarks. Laurie (1988) revised *Onymagnostus* Öpik, recognizing *O. semiermis* Öpik 1979, *O. hybridus* (Brögger, 1878), *O. mundus* Öpik 1979 and *O. seminula* (Whitehouse 1939) as valid species. The Gowers specimens are assigned to *Onymagnostus semiermis* on the basis of a more transverse cephalon, more elongate basal lobes, less expanded and more clearly furrowed posterior glabellar lobe, the longer, narrower pygidial axis and the minute pygidial spines.

Figure 3-7 *Onymagnostus semiermis*: **A.** entire specimen CPC XXXXX, from GF2, level 15.8, showing scrobiculation, x 9.4; **B.** entire specimen CPC XXXXX, with damaged cephalon, from GF2, level 12.2, x 10.0; **C.** entire specimen CPC XXXXX with damaged thorax, from GF2, level 10, x 5.8; **D.** entire young specimen CPC XXXXX, from GF2, level 12.2, with damaged cephalon and thorax, narrower pygidial axis, x 15.5; **E –T** are cephalae: **E.** CPC XXXXX, from GF2, level 12.2, x 6.2; **F.** CPC XXXXX, from GF2, level 10, x 11.2; **G.** CPC XXXXX, from GF2, level 17.6, flattened specimen, x 13.1; **H.** CPC XXXXX, from GF1, level 59.7, exfoliated on the right-hand side, x 6.2; **I.** CPC XXXXX, from GF2, level 13.7, showing scrobiculation, x 13.1; **J.** CPC XXXXX, from GF2, level 12.2, with wide genae and attached thorax, x 7.5; **K.** CPC XXXXX, from GF2, level 12.2, showing scrobiculation, x 7.5; **L.** CPC XXXXX, from GF2, level 12.2, showing scrobiculation, x 6.5; **M.** CPC XXXXX, from GF2, level 12.2, x 6.9; **N.** CPC XXXXX, broken specimen, from GF2, level 10, x 7.4; **O.** CPC XXXXX, from GF2, level 15.8, showing faint scrobiculation, x 10.6; **P.** CPC XXXXX, from GF2, level 10, x 8.6; **Q.** CPC XXXXX, from GF2, level 10, with crack in upper right genae, x 7.7; **R.** CPC XXXXX, from GF2, level 13.7, showing pitted type scrobiculation, x 13.1; **S.** CPC XXXXX, from GF1, level 59.7, exfoliated, x 12.2; **T.** CPC XXXXX, from GF2, level 17.6, with wide genae, x 6.6.



Figure 3-7 *Onymagnostus semiermis*

Figure 3-8. *Onymagnostus semiermis* pygidia: **A.** CPC XXXXX, from GF2, level 12.2, x 6.6; **B.** CPC XXXXX, from GF2, level 12.2, x 6.6; **C.** CPC XXXXX, from GF2, level 10, x 8.1; **D.** CPC XXXXX, from GF2, level 10, x 7.3; **E.** CPC XXXXX, from GF2, level 12.2, x 9.3; **F.** CPC XXXXX, from GF2, level 10, x 9.3; **G.** CPC XXXXX, from GF2, level 10, crack in exoskeleton, x 5.5; **H.** CPC XXXXX, from GF2, level 12.2, x 7.9; **I.** CPC XXXXX, from GF2, level 12.2, x 7.6; **J.** CPC XXXXX, from GF2, level 10, x 6.8; **K.** CPC XXXXX, from GF2, level 12.2, x 5.0; **L.** CPC XXXXX, from GF2, level 12.2, x 16.7; **M.** CPC XXXXX, from GF2, level 10, x 10.6; **N.** CPC XXXXX, from GF2, level 10, x 8.2; **O.** CPC XXXXX, from GF2, level 10, x 7.4; **P.** CPC XXXXX, from GF2, level 10, x 6.9; **Q.** CPC XXXXX, from GF2, level 13.7, x 19.4; **R.** CPC XXXXX, from GF2, level 10, x 7.7; **S.** CPC XXXXX, from GF2, level 12.2, x 6.3; **T.** CPC XXXXX, from GF1, level 41.3, young specimen x 12.9; **U.** CPC XXXXX, from GF1, level 64.9, young specimen with wide border, x 18.4; **V.** CPC XXXXX, from GF2, level 13.7, x 10.7; **W.** CPC XXXXX, from GF2, level 10, distorted specimen, x 6.0; **X.** CPC XXXXX, from GF2, level 13.7, x 6.9.

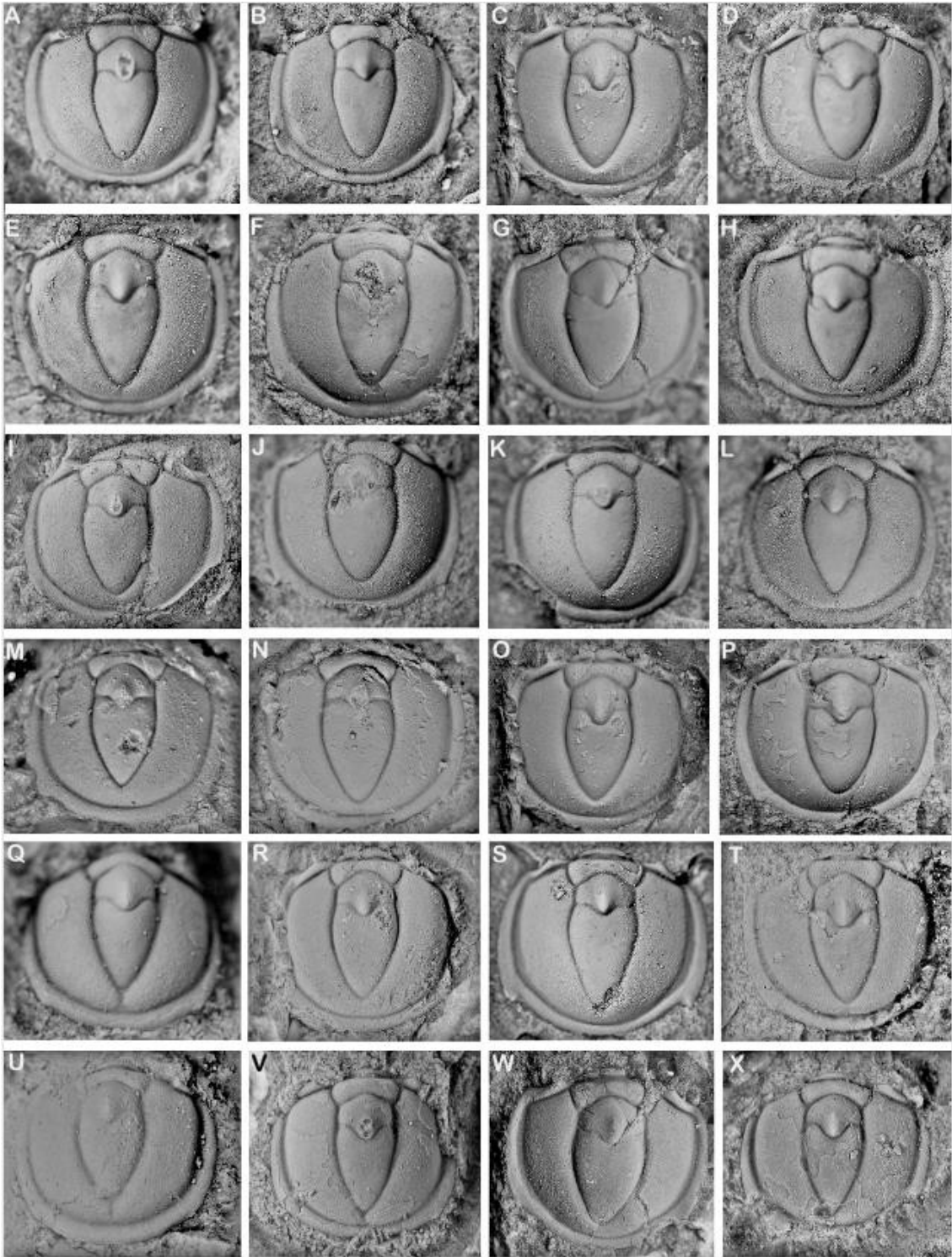


Figure 3-8 *Onymagnostus semiermis*

Tomagnostus Howell, 1935a

Type species. *Aagnostus fissus* Lundgren in Linnarsson, 1879, by original designation; Exsulans Limestone, *T. gibbus* Zone, Sweden.

Diagnosis. See Shergold & Laurie (1997, p. 354).

3.4.3. *Tomagnostus fissus* (Lundgren in Linnarsson 1879) (Fig. 3-9)

2013 *Tomagnostus fissus* Weidner & Neilsen, p. 21 (cum. syn.)

Material. CPC TF1-4; Four pygidia, GF1: 34.6, GF2: 13.7; upper *T. gibbus* Zone to lower *A. atavus* Zone.

Remarks. Despite the lack of an associated cephalon, these specimens are confidently assigned to *T. fissus* due to their characteristic subelliptical pygidial shape, the depressed pygidial posteroaxis with the transverse furrow and small secondary node placed anteriorly (Fig. 3-9A, C, D). The four Gowers specimens closely resemble the topotype pygidium illustrated by Shergold and Laurie (1997, Fig. 224, 3b), see also Robison (1994, Fig. 30.1) and Weidner & Neilsen (2013, fig. 19C, D). Two small specimens from the Gowers Formation (Figs 3-9A, D) show the characteristic pair of small tubercles side-by-side on the anterior lobe (see Westergård 1946, pl. 7, fig. 29). The Gowers specimens represent the first record of this species in Australia.

Figure 3-9. *Tomagnostus fissus*: **A.** pygidium CPC XXXXX, from GF2, level 13.7, x 14.3; **B.** pygidium CPC XXXXX, from GF2, level 13.7, x 20.5; **C.** pygidium CPC XXXXX, from GF2, level 13.7, x 19.1; **D.** pygidium CPC XXXXX, from GF1, level 34.6, x 12.1

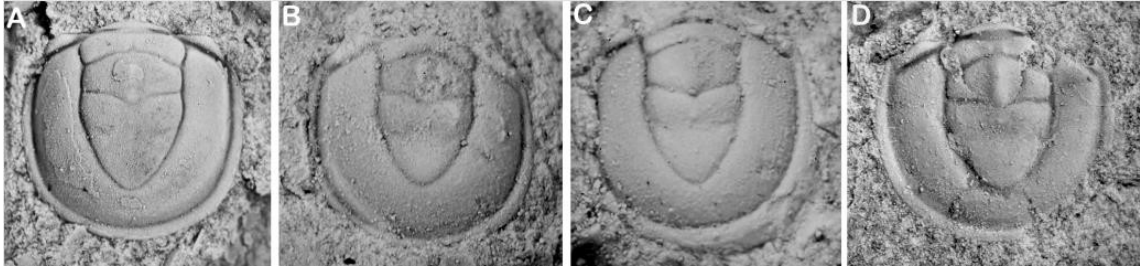


Figure 3-9. *Tomagnostus fissus*

Triplagnostus Howell 1935a

?1936 *Solenagnostus* Whitehouse 1936, p. 86

1979 *Triplagnostus* (*Aristarius*) Öpik, p. 125 Type species. *Aagnostus gibbus* Linnarsson 1869

Diagnosis. See Laurie (1988, p. 194).

3.4.4. *Triplagnostus gibbus* (Linnarsson, 1869) (Fig. 3-10A-T, Fig. 3-11A-W)

1997 *Triplagnostus gibbus* (Linnarsson 1869), Buchholz, p. 255.

2008 *Ptychagnostus gibbus* (Linnarsson 1869), Høyberget & Bruton, pp. 51–53, pl. 8, figs N–S. (cum. syn.)

Material. CPCXXTG1-42. 27 cephalae, 17 pygidia. GF1: 46.9–76, GF2: 12.2–17.6; *T. gibbus* to lower *A. atavus* Zone.

Diagnosis. See Laurie (1988, p. 196).

Remarks. The Gowers specimens show the characteristic cephalae with a slender, segmented and almost parallel-sided posteroglabella and a pair of posterior cephalic spines (see Fig. 3-10). The pygidia of *T. gibbus* from the Gowers have a median postaxial furrow and a large pygidial node (see Fig. 3-11). The abundant specimens in the Gowers Formation add some detail to the morphologic and ontogenetic information on this species.

Høyberget and Bruton (2008) found Norwegian species to have diagnostic characters which varied little but the length of cephalic spines and basal lobes did vary slightly. It is not possible to assess the cephalic spines of the majority of the Gowers specimens as they have broken off 24 of the 26 adult specimens - the remaining two are similar in their dimensions and with specimens from other localities. There does appear to be slight variation

in the size of the posterior part of the basal lobe, being wider in some specimens, although this does not appear to be ontogenetic. The Gowers specimens display variation in other characters, for example – the F3 furrow varies from straight to curved slightly posteriorly and the length of the postaxial median furrow varies from 13 to 23% (N = 12) of pygidial length and is not ontogenetically related as Robison (1982) proposed (with 20% occurring in the smallest specimen (Fig. 3-11U) and 23% in a large specimen). Robison proposed that the triangular anterior lobe is more pointed anteriorly in meraspids, but is consistently 30-31% (n =10) of glabellar length in both adult and juvenile Gowers specimens. The pair of pygidial swellings or incipient spines at posterolateral corners appear to be ontogenetically related as the smallest specimen in the Gowers - Fig. 3-11U - has no pygidial swellings. The secondary node is usually conspicuous and almost always halfway between F2 and the axis termination, and is the same in the smallest specimen. This node is not visible in the Norwegian material (Høyberget and Bruton, 2008) but appears to be in a similar position in the specimens from the United States (Robison, 1982) and in previously illustrated Australian material (Laurie, 1988).

Figure 3-10. *Triplagnostus gibbus* (juvenile specimens): **A – J, L,** are cephala, **K, M – T** are pygidia. **A.** CPC XXXXX, from GF1, level 46.9, surface exfoliated, x 12.1; **B.** CPC XXXXX, from GF1, level 64.9, x 10.9; **C.** CPC XXXXX, from GF1, level 64.9, broken anterior and axis, x 14.3; **D.** CPC XXXXXX, from GF1, level 59.7, axis partly exfoliated, x 13.3; **E.** CPC XXXXX, from GF2, level 17.6, x 10.3; **F.** CPC XXXXX, from GF2, level 17.6, partly exfoliated, x 16.7; **G.** CPC XXXXX, from GF1, level 53.3, mostly exfoliated, x 11.7; **H.** CPC XXXXX, from GF1, level 53.3, x 11.6; **I.** CPC XXXXX, from GF1, level 53.3, x14.1; **J.** CPC XXXXX, from GF1, level 53.3, x10.7; **K.** CPC XXXXX, from GF1, level 56.3, x 12.1; **L.** CPC XXXXXX, from GF1, level 64.9, x 13.8; **M.** CPC XXXXX, from GF1, level 59.7, exfoliated specimen, x 14.8; **N.** CPC XXXXXX, from GF1, level 64.9, with wide axis, x 11.7; **O.** CPC XXXXX, from GF1, level 64.9, x 10.9; **P.** CPC XXXXXX, from GF1, level 64.9, x 12.4; **Q.** CPC XXXXXX, from GF1, level 64.9, x 11.4; **R.** CPC XXXXX, from GF1, level 64.9, x 9.6; **S.** CPC XXXXX, from GF1, level 59.7, x 11.8; **T.** CPC XXXXX, from GF1, level 64.9, very small specimen x 25.

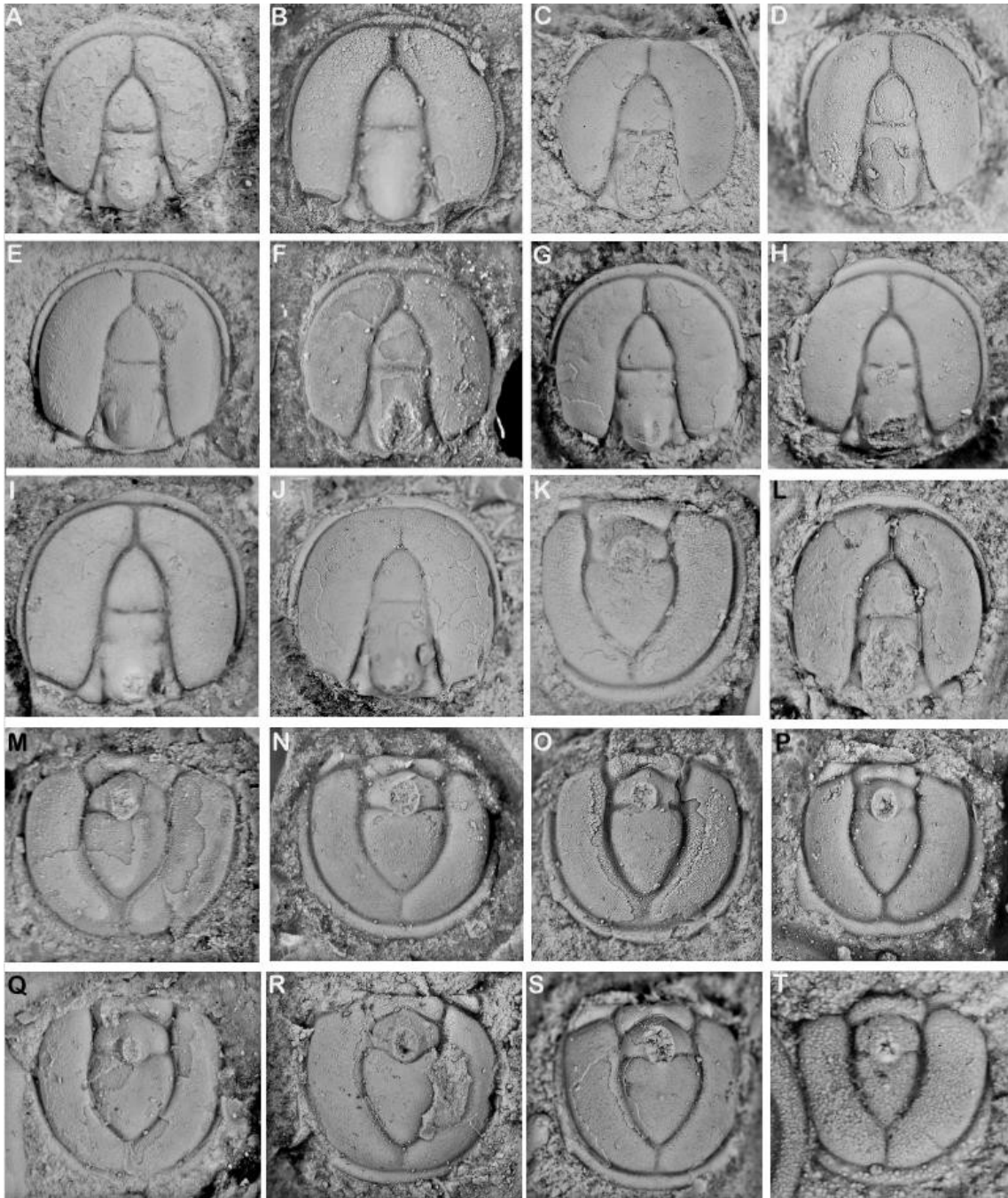


Figure 3-10. *Triplagnostus gibbus* (juvenile specimens)

Figure 3-11. *Triplagnostus gibbus* (adult specimens except for U): **A.** ?complete specimen x 8.1; **B – O** are cephalata: **B.** x10.6; **C.** x11.1; **D.** x 13.1; **E.** x11.6; **F.** x 11.3; **G.** x 11.3; **H.** x 9.5; **I.** x 10.6; **J.** x7.7; **K.** x 14; **L.** x 9.0; **M.** x 11.9; **N** x11.6; **O.** x11.4; **P – W** are pygidia: **P.** x 10.8; **Q.** x 1.9; **R.** x5.6; **S.** x 9.7; **T.** x 10; **U.** (juvenile) x 14.6; **V** x 10.6; **W.** x 10.6.

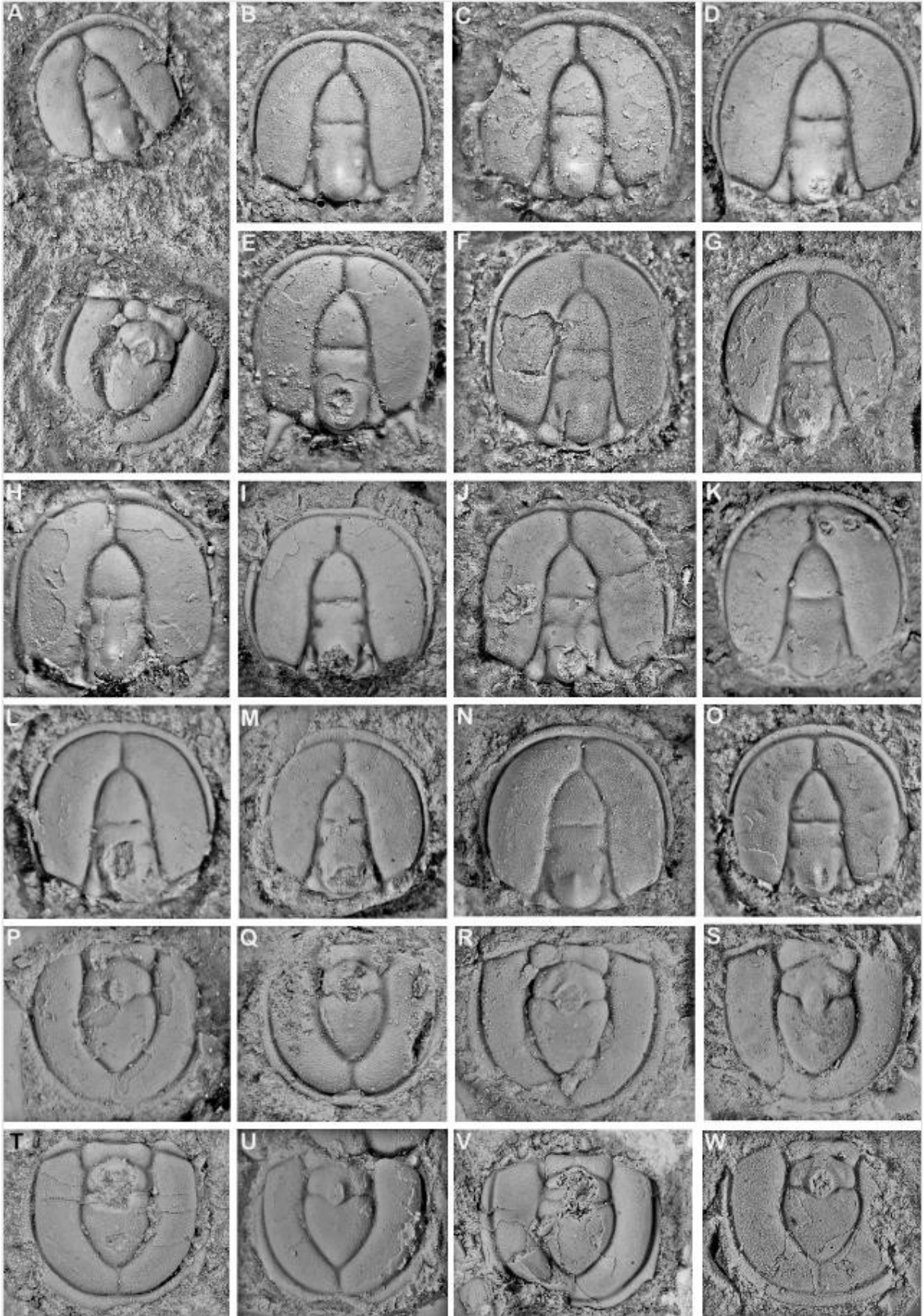


Figure 3-11. *Triplagnostus gibbus* (adult specimens except for U)

Zeteagnostus Öpik, 1979

Type species. *Zeteagnostus incautus* Öpik, 1979, from western Queensland, Australia.

Diagnosis. See Laurie 1988, p. 176.

Remarks. Laurie (1988) differentiated *Zeteagnostus* from *Ptychagnostus* due to the smooth prosopon, strongly expanded posterior glabellar lobe with the node located near the midlength or in the posterior half of the posterior lobe, the poorly defined basal lobes, the very small pygidial axial node with a weakly deflected or undeflected F2 furrow and a weakly defined F1 furrow. Laurie also questioned Öpik's use of the rudimentary basal lobes and terminal pygidial node as diagnostic characters of *Zeteagnostus*, interpreting the curved shape of the basal furrow to represent a division of the anterior and posterior part of the lobes and finding that the terminal pygidial node is not usually present.

3.4.5. *Zeteagnostus sinicus* (Lu, 1957) (Fig. 3-12A-T, Fig. 3-13A-T)

1988 *Zeteagnostus scarifatus* (Öpik); Laurie, p. 178 (cum. syn.) 1988 *Zeteagnostus scarifatus* (Öpik); Laurie, p. 178, Fig. 4A-H

Material. CPCXXZS1-44; 20 cephalae, 24 pygidia; GF1: 49–64.9, GF2: 10–15.8; T. gibbus to lower A. atavus Zone.

Description. Exoskeleton of small to medium size, commonly scrobiculate; prosopon smooth. Cephalon subcircular, width approximately equal to length in both juveniles and adults, moderately convex. Glabella width 46–61% length (n =15), usually 50%; posterior glabellar lobe strongly expanded, strongly to very strongly tapered, anterior lobe subtriangular, F1 undeveloped, F2 furrows rarely evident, F3 straight or curved slightly posteriorly; glabellar

node near midpoint of posteroglabella or rarely slightly anterior to midpoint. Elongated triangular basal lobes, divided, commonly indistinct anteriorly. Basal furrows well-defined.

Thorax unknown.

Pygidium subcircular, width approximately equal to length (n = 18), moderately to highly convex; median node weak, F2 almost straight or weakly deflected anteriorly, F1 deflected weakly forward; M2 pentagonal; posteroaxis weakly ogival; postaxial median furrow present, longer in meraspides (Fig. 3-13X) and becoming shorter or weakly defined in adult stage; no M2 until pygidium reaches ca. 1.2 mm long (as shown by Fig. 3-13F, X, W). The posteroaxis extremity tends to become less rounded after development of the M2. Pygidial node rarely present but is situated posteriorly on the posteroaxis when it is (Fig. 3-13B, I, L).

Remarks. The type specimens of *Zeteagnostus sinicus* Lu are poorly preserved and debate over their relationship with *P. intermedius* (Tullberg, 1880) has continued since Laurie (1988) questioned the assignment of *P. intermedius*. Recently, Ahlberg *et al.* (2007) reviewed the type species and reassigned Laurentian agnostids previously assigned to *P. intermedius* by Robison (1982, 1984, 1994) and Rowell *et al.* (1982) to *P. sinicus* Lu, 1957. They also found that *P. scarifatus* Öpik 1979 is a junior subjective synonym of *P. sinicus*.

Figure 3-12. *Zeteagnostus sinicus* cephalae: **A.** CPC XXXXX, from GF1, level 64.9, showing scrobiculation, x 14.5; **B.** CPC XXXXX, from GF1, level 59.7, x 17.8; **C.** CPC XXXXX, from GF1, level 64.9, weakly scrobiculate x15.0; **D.** CPC XXXXX, from GF1, level 64.9, damaged exoskeleton, x 13.0; **E.** CPC XXXXX, from GF1, level 64.9, x 16.8; **F.** CPC XXXXX, from GF1, level 64.9, x 13.6 **G.** CPC XXXXX, from GF1, level 64.9, weakly scrobiculate, x 9.7 **H.** CPC XXXXX, from GF1, level 64.9, showing scrobiculation, broken anterior, x 9.4; **I.** CPC XXXXX, from GF1, level 59.7, weakly scrobiculate, x 12.1; **J.** CPC XXXXX, from GF1, level 64.9, x 12.1; **K.** CPC XXXXX, from GF1, level 64.9, x 21.3; **L.** CPC XXXXX, from GF1, level 64.9, weakly scrobiculate, x 10.6; **M.** CPC XXXXX, from GF1, level 49, showing scrobiculation, x 14.6; **N.** CPC XXXXX, from GF1, level 64.9 x 21.3; **O.** CPC XXXXX, from GF1, level 64.9, damaged exoskeleton, x 10.6; **P.** CPC XXXXX, from GF1, level 59.7, x 13.6; **Q.** CPC XXXXX, from GF1, level 64.9, x 11.3; **R.** CPC XXXXX, from GF1, level 59.7, x 21.9; **S.** CPC XXXXX, from GF1, level 59.7, x 21.1; **T.** CPC XXXXX, from GF1, level 49, showing scrobiculation, x 11.4.

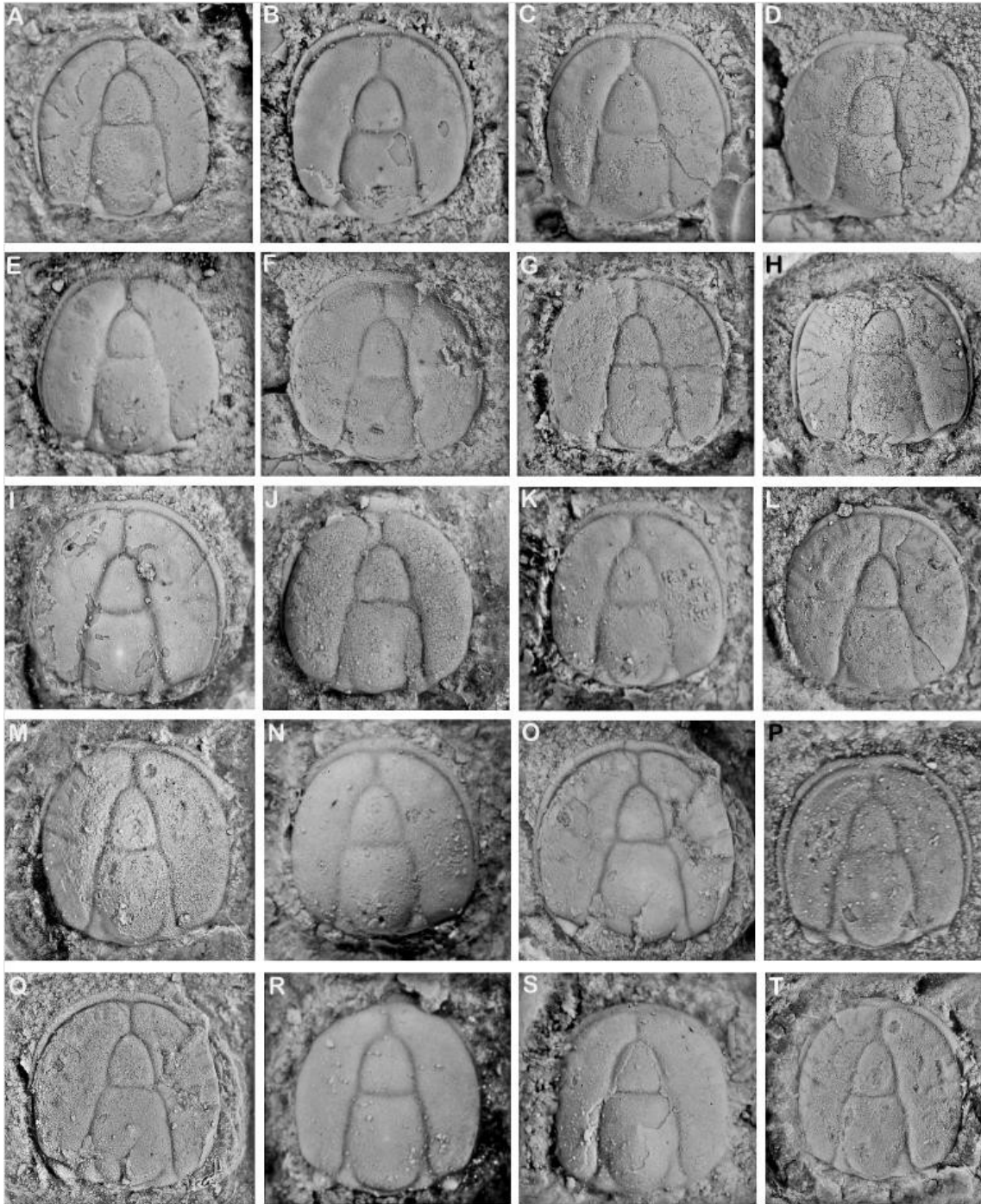


Figure 3-12. *Zeteagnostus sinicus*

Figure 3-13. *Zeteagnostus sinicus* pygidia: **A.** CPC XXXXX, from GF1, level 64.9, x 12.3; **B.** CPC XXXXX, from GF1, level 49, showing wide border, x13.0; **C.** CPC XXXXX, from GF1, level 59.7, x 13.0; **D.** CPC XXXXX, from GF1, level 59.7, x 13.2; **E.** CPC XXXXX, from GF1, level 64.9, x13.8; **F.** CPC XXXXX, from GF1, level 64.9, x 25.4; **G.** CPC XXXXX, from GF1, level 64.9, x 16.8; **H.** CPC XXXXX, from GF1, level 64.9, x 15.2; **I.** CPC XXXXX, from GF1, level 64.9, x 13.5; **J.** CPC XXXXX, from GF1, level 64.9, x 13.9; **K.** CPC XXXXX, from GF2, level 15.8, x16.8; **L.** CPC XXXXX, from GF1, level 59.7, showing wide border, x 24.3; **M.** CPC XXXXX, from GF1, level 64.9, x 13.0; **N.** CPC XXXXX, from GF1, level 64.9, slightly damaged, x 13.9; **O.** CPC XXXXX, from GF1, level 64.9, x 13.1; **P.** CPC XXXXX, from GF1, level 64.9, x 12.9; **Q.** CPC XXXXX, from GF1, level 64.9, damaged exoskeleton, x 13.0; **R.** CPC XXXXX, from GF1, level 64.9, small specimen showing a shorter axis with rounded tip, x 23.6; **S.** CPC XXXXX, from GF1, level 64.9, x 14.2; **T.** CPC XXXXX, from GF1, level 59.7, x 15.9; **U.** CPC XXXXX, from GF1, level 64.9, x 13.6; **V.** , CPC XXXXX, from GF1, level 64.9x 14.1; **W.** CPC XXXXX, from GF1, level 59.7, meraspid (M1), showing a shorter axis with rounded tip x 31.8; **X.** CPC XXXXX, from GF1, level 64.9, meraspid (M0), showing a shorter axis with rounded tip, x 33.3.

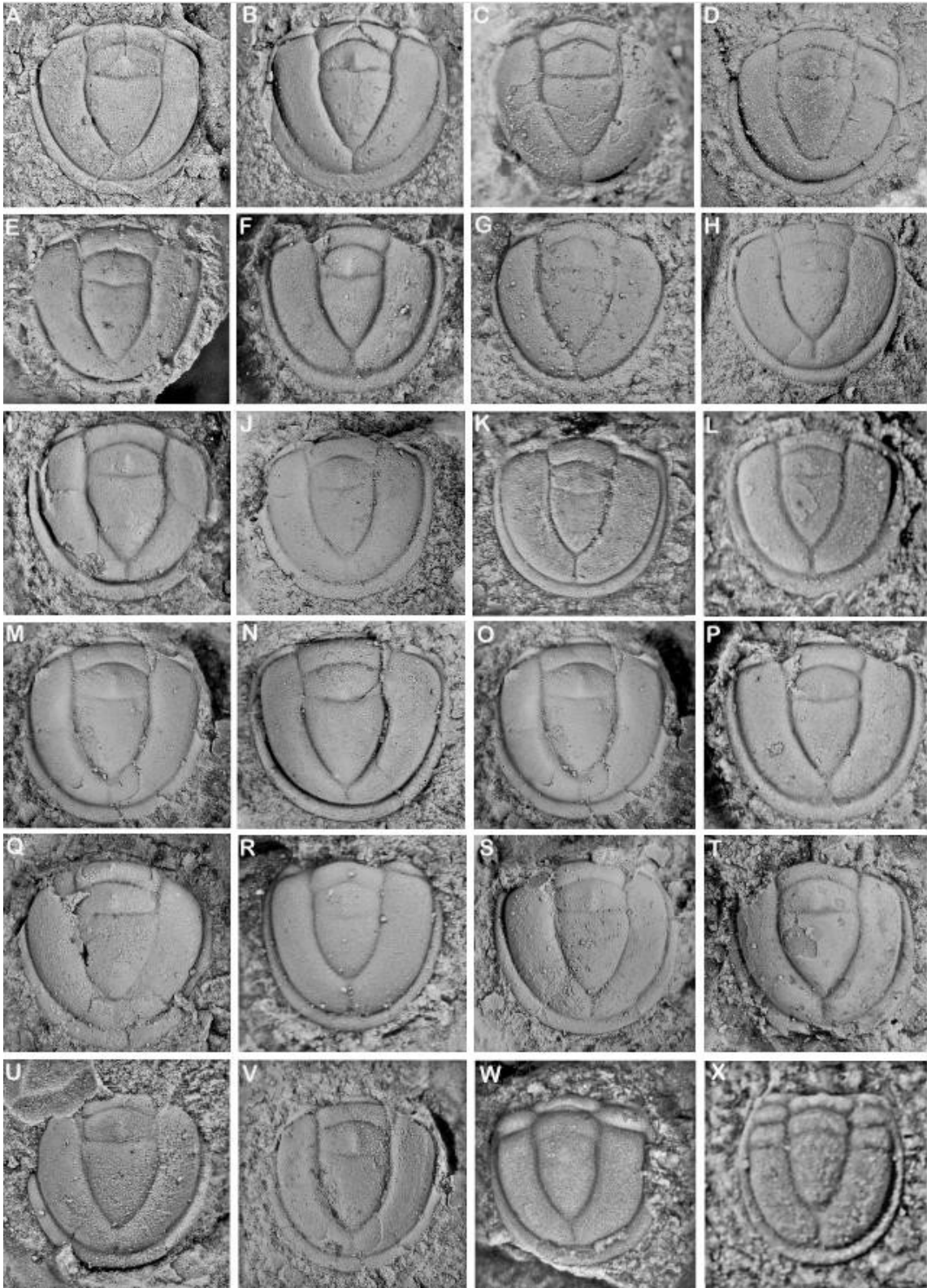


Figure 3-13. *Zeteagnostus sinicus*

This is followed here, but as Laurie (1988) argued, *Zeteagnostus* should be kept a separate genus from *Ptychagnostus* due to the smooth prosopon, strongly expanded posteroglabella, poorly defined basal lobes, very small pygidial axial node with a weakly deflected or undeflected F2 furrow and a weakly deflected F1 furrow.

Family **Spinagnostidae** Howell, 1935b

Hypagnostus Jaekel, 1909

2011 *Hypagnostus*; Jago *et al.*, p. 24 (cum. syn.)

Type species. *Aagnostus parvifrons* Linnarsson, 1869, by original designation;

Hypagnostus parvifrons Zone; Västergötland, Sweden.

Diagnosis. See Høyberget and Bruton (2008, p. 36).

Remarks. For a comprehensive discussion of the genus, see Høyberget and Bruton (2008).

Sun *et al.* (2013) provide the most recent treatment of the genus.

3.4.6. *Hypagnostus parvifrons* (Linnarsson, 1869) (Fig.3-14A- O)

1979 *Hypagnostus fatkai* sp. nov.; Kordule & Šnajdr: 45, pl. 1, figs a–c. 1981 *Hypagnostus jincensis* n. sp.; Fatka *et al.*, p. 367 [*partim*], pl. 2, fig. 1.

1992 *Hypagnostus* cf. *parvifrons* (Linnarsson); Fatka & Kordule, pl. 2, fig. 1. 2000

Hypagnostus parvifrons, Peng & Robison, p. 60–62 (cum. syn.)

2013 *Hypagnostus parvifrons* Weidner & Nielsen, p. 26 (cum. syn.)

Material and occurrence. CPCXX-XX, 11 cephalae, 5 pygidia, GF1: 59.7–62.2; lower

A. atavus Zone.

Remarks. Öpik (1979) documented limited material of *Hypagnostus parvifrons* from the Currant Bush Limestone but new material from the Gowers Formation (of which over 30 specimens have been collected) provides a better understanding of this taxon in Australia. The Gowers specimens support the fact that *Hypagnostus parvifrons* is a variable species, especially in pygidial morphology, as noted by Westergård (1946), Robison (1964), Peng and Robison (2000) and Westrop *et al.* (1996). Noted variable characters are the taper of the anterolateral glabella, the shape of F3, smooth genae or those with weak scrobiculation, and pygidial axis length. The Gowers specimens show variation in these characters but fall well within the limits of variation noted by Peng & Robison (2000). The glabella occupies 45 to 51% of the cephalic length and the F3 varies from straight (Fig. 3-14A) to curved (Fig. 3-14C). The pygidial axis varies from 67 to 73% of pygidial length which is shorter than in the specimens from Hunan (Peng & Robison, 2000) and Antarctica (Jago and Cooper, 2007). The secondary pygidial nodes in the Gowers specimens are placed more forward than in the specimens from Hunan (Peng & Robison, 2000) and Norway (Høyberget and Bruton, 2008). The four illustrated Gowers pygidia show the characteristic forward projection of the posterior border. The posterior border furrow extends forwards and reaches the pygidial axis. (Fig.3-14L - O).

However, the variation in the position of the weak glabellar node has not been previously discussed. The glabellar nodes in the Gowers specimens are all situated ca. 40% of the distance from F3 to the posteroglabella extremity, but the nodes of the Hunan specimens for example, are positioned more anteriorly, about halfway between F3 and the posterior extremity (Peng and Robison, 2000, Fig. 45.1, 45.4, 45.8). The nodes visible on two Newfoundland specimens (Westrop *et al.*, 1996, Fig. 23.3, 23.5) appear to be situated at the mid-length Westrop *et al.* (1996). One Antarctic specimen from Reilly Ridge (Jago and

Cooper, 2007, fig. 2H) appears to have the node in the same position as the Gowers specimens. The one illustration of *H. parvifrons* from Greenland (Robison, 1994) does not show a glabellar node nor does the one cephalon illustrated by Weidner and Neilsen (2013) from Denmark. The cephalon from Norway (Høyberget and Bruton, 2008) have the node about one-third of distance from F3 to the extremity of the posteroglabella. The cephalic node is difficult to assess in the illustrations by Sun *et al.* (2013) of specimens from the Warburton Basin.

Hypagnostus parvifrons has been restricted to forms which possess an expanded pygidial border behind the axis as shown in Fig. 3-14 M–O. The four Gowers pygidia show little variation in the pygidial axis length as do the Newfoundland specimens illustrated by Westrop *et al.* (1996). One Gowers pygidium (Fig. 3-14L) has a less expanded border but pygidia from Newfoundland (Westrop *et al.*, 1996, fig. 23.1-23.11) show variation in border width and include forms in which expansion is weak or absent.

Figure 3-14. *Hypagnostus parvifrons*: **A.** matching cephalon and pygidium, CPC XXXXX, from GF1, level 59.7, x 8.4; **B – K** are cephala: **B.** CPC XXXXX, from GF1, level 62.2, x 15.5; **C.** CPC XXXXX, from GF1, level 62.2, x 11.4; **D.** CPCXXXXX, from GF1, level 59.7, x 7.9; **E.** CPC XXXXX, from GF1, level 59.7, x 12.0; **F.** CPC XXXXX, from GF1, level 59.7, x 7.9; **G.** CPC XXXXX, from GF1, level 59.7, x 14.5; **H.** CPC XXXXX, from GF2, level 20.8, partially exfoliated, x 11.0; **I.** CPC XXXXX, from GF1, level 62.2, partially exfoliated, x 9.2; **J.** CPC XXXXX, from GF1, level 59.7, mostly exfoliated, x 11.9; **K.** CPC XXXXX, from GF1, level 62.2, x 7.5; **L – O** are pygidia: **L.** CPC XXXXXX, from GF1, level 59.7, x 10.3; **M.** CPC XXXX, from GF1, level 62.2, x 10.0; **N.** CPC XXXXX, from GF1, level 62.2, x 11.5; **O.** CPC XXXXXX, from GF1, level 62.2, x 13.8.

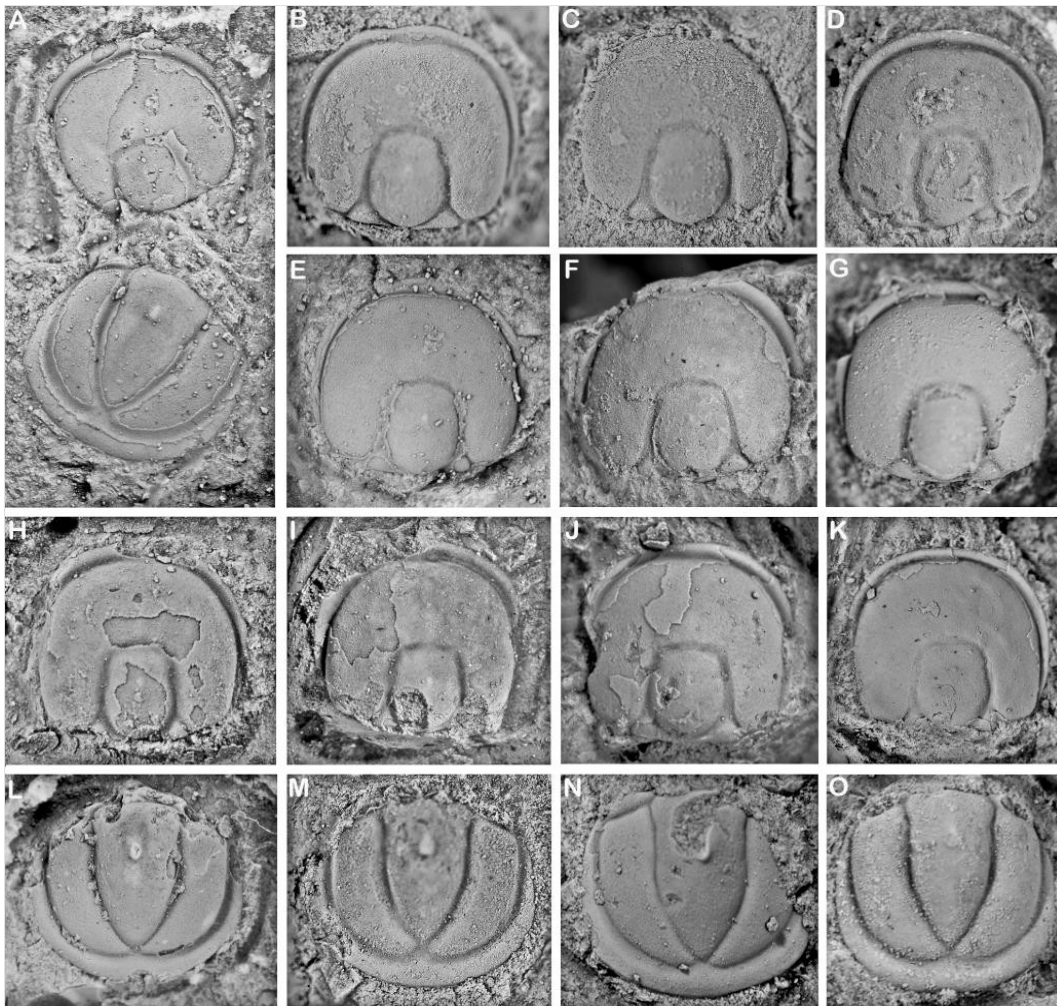


Figure 3-14. *Hypagnostus parvifrons*

For this reason, Westrop *et al.* (1996) regarded *H. clipeus* as a junior subjective synonym of *H. parvifrons* and considered the poorly known *H. vortex* Whitehouse, which also possesses a narrow pygidial border, to also most likely be a synonym of *H. parvifrons*. As stated by Høyberget and Bruton (2008), *H. clipeus* Whitehouse 1939, lacks the expanded pygidial border, possesses a node at the tip of the pygidial axis and occurs stratigraphically higher, so is retained as a separate species by these authors.

***Euagnostus* Whitehouse, 1936**

Type species. *Euagnostus opimus* Whitehouse, 1936, by original designation; Currant Bush Limestone, Queensland, Australia (for redescription, see Jell and Robison, 1978).

Diagnosis. See Shergold and Laurie (1997, p. 356).

Remarks. Characterisation of this genus has been problematic, with Jell and Robison (1978) placing *Euagnostus* in synonymy with *Peronopsis* Hawle & Corda, 1847, based on the type species *Battus integer* Beyrich, 1845. *Peronopsis*, which incorporates over 100 species, has been a “wastebasket taxon” for any Cambrian agnostid with a bilobate glabella, no median preglabellar furrow and a lobate pygidial axis (See discussions by Laurie (2004), Naimark (2012) and Weidner and Neilsen (2013)).

The original Queensland material of *E. opimus*, described by Whitehouse (1936) contained more than one species and was later revised by Jell and Robison (1978), then Öpik (1979) whose designation also included specimens of *Doryagnostus deltoides*, *D.* sp. nov. and *Acadagnostus rakuroensis* (as ‘*Baltagnostus*’ *australis*) (see Laurie 2004, p. 245). Weidner and Nielsen (2013) adopted the separation of *Peronopsis* and *Euagnostus*, following Shergold and Laurie (1997); - also see remarks by Høyberget and Bruton (2008, p. 26).

3.4.7. *Euagnostus interstrictus* (White, 1874) (Fig. 3-15A-X, Fig. 3-16A-X)

2006 *Euagnostus inetrstrictus*, Laurie, p. 142 (cum. syn.)

2006 *Euagnostus* aff. *interstrictus* Laurie, p. 143, Fig. 16.

2013 *Euagnostus* aff. *interstrictus* Weidner and Nielsen, p. 33, Fig. 27A–F.

Diagnosis. See Laurie (2006, p. 142)

Material. CPCXXE11- 48, 24 cephalata, 24 pygidia from GF1: 11.2–62.2, GF2: 1.2–20.8;

T. gibbus to lower *A. atavus* Zones.

Description. Large agnostid, cephalon and pygidium reaching over 6mm length; nonscrobiculate, surface smooth. Cephalon rounded to quadrate in outline, L: W = 82–98% (av. 89%, n = 23), nonspinose, moderately convex; border fairly narrow, roll-like; border furrow well-defined, narrow to medium width; glabella 70–79% (av. = 74%, n = 22) as long as cephalon; anterior glabellar lobe semioval, broadly rounded anteriorly, occupying 32–39 (av. = 35%, n = 22) of glabellar length. Posterior glabellar lobe variable in expansion; F1 and F2 absent or very weakly developed as slight lateral notches. F3 well defined, usually straight but sometimes very slightly curved rearwards, sometimes deeper laterally than medially. Glabellar node variably positioned but usually ca. midlength of posterior glabellar lobe. Basal lobes very short, transverse.

Thorax unknown.

Pygidium rounded to weakly quadrate in outline, L: W = 82–97% (av. 90%, n = 24), with posterolateral swellings in juveniles developing into very small posterolateral spines in adult specimens, moderately convex; border wide in juveniles but of moderate width in adults,

border furrow distinct, of variable width, commonly widest posterolaterally. Sometimes acrolobe has a slight indentation behind axis; postaxial median furrow clearly developed, shortening in length (sag.) with maturity. Axis about 59% as wide as long and about 75% as long as pygidium, moderately convex, not extending to border furrow, slightly constricted across F1, widest across M1 lobe. Posterior extremity angular, broadly acute to right-angled; axial node of moderate size; F1 and F2 largely effaced, only developed as indentations in side of axis; M1 broad, lateral margins convex; M2 constricted; posteroaxis ogival, with maximum width near F2.

Remarks. *Euagnostus interstrictus* is very abundant in the Gowers Formation and shows considerable morphological and ontogenetic variability. Several of the Gowers specimens reach a much larger size than given in Laurie's (2004, 2006) descriptions which states the cephalon and pygidia reach 3.5 or 4mm. The Gowers specimens have an average cephalic length of 5.0mm (N = 21) and average pygidial length = 5.1mm (n = 24). The axis width: length varies in the Gowers specimens, from 54–67% (av. = 61%, n = 23), which incorporates the 59% value for *E. aff. interstrictus* given by Laurie (2004). The Gowers specimens show the small variability in the glabellar node, with the juvenile specimens (Fig. 3-15L, O, X) showing the node in a more posterior position. The width of the pygidial border and the shape of the pygidial axis are also shown to be variable traits, both ontogenetically and morphologically, with three juvenile specimens (Fig. 3-16A, F, Q) showing the narrower axis and wider pleurae as well as a slightly longer median furrow. The presence/absence of the pygidial spines has been used to differentiate *E. interstrictus* from *E. aff. interstrictus*, but this also appears to be a highly variable trait and the juvenile specimens have swellings rather than spines. Pygidial swellings are the usual feature in the Gowers specimens. The length of the pygidial axis is also shown to be a highly variable

feature, with the three juvenile specimens having a short axis, but also varying amongst the adult specimens (compare Fig. 3-16E and Fig. 3-16V).

The specimens assigned to *E. interstrictus* (Robison, 1964, Pl. 82, figs 13-15, 18) show a similar variation in pygidial axis length. Some specimens (e.g. Robison 1964, pl. 82, figs 13-15) are small in size and their pygidial axes do not reach the border while larger specimens (e.g. Robison 1964, pl. 82, fig. 18) have a much longer axis. However, the larger specimens of *E. interstrictus* from Greenland (Robison 1994, fig. 19-9, 19-10) also have a shorter axis. Specimens of *E. interstrictus* illustrated by Fritz and Simandl (1993, pl. 1, figs 6, 7, 15) are adults with long axes. The two pygidia from western Newfoundland (Westrop *et al.* 1996, fig. 22-2, 22-3) show long axes and are quite large specimens.

Figure 3-15. *Euagnostus interstrictus* cephalae: **A.** CPC XXXXX, from GF1, level 49, partially exfoliated, x 6.0; **B.** CPC XXXXX, from GF2, level 13.7, partially exfoliated, x 6.8; **C.** CPC XXXXX, from GF2, level 13.7, partially exfoliated, x 7.0; **D.** CPC XXXXX, from GF1, level 46.9, showing ‘kink’ in anterior, x 8.5; **E.** CPC XXXXX, from GF2, level 13.7, partially exfoliated, x 8.1; **F.** CPC XXXXX, from GF2, level 7, broken specimen, x 10.0; **G.** CPC XXXXX, from GF2, level 13.7, x 6.0; **H.** CPC XXXXX, from GF2, level 13.7, showing ‘kink’ in anterior, broken anterolateral corner and slight exfoliation, x 7.0; **I.** CPC XXXXX, from GF1, level 49, some exfoliation, x 7.4; **J.** CPC XXXXX, from GF2, level 13.7, exfoliated and slightly distorted specimen, x 7.8; **K.** CPC XXXXX, from GF1, level 53.3, partially exfoliated, x 7.6; **L.** CPC XXXXX, from GF1, level 53.3, partially exfoliated, x 10.6; **M.** CPC XXXXX, from GF2, level 13.7, showing ‘kink’ in anterior, x 6.7; **N.** CPC XXXXX, from GF2, level 7, showing slight ‘kink’ in anterior, x 9.0; **O.** CPC XXXXX, from GF1, level 53.3, showing slight ‘kink’ in anterior, x 9.7; **P.** CPC XXXXX, from GF2, level 13.7, x 6.3; **Q.** CPC XXXXX, from GF1, level 53.3, partially exfoliated straight anterior, x 7.1; **R.** CPC XXXXX, from GF2, level 13.7, partially exfoliated, x 7.2; **S.** CPC XXXXX, from GF2, level 13.7, partially exfoliated, x 6.9; **T.** CPC XXXXX, from GF1, level 53.3, x 8.4; **U.** CPC XXXXX, from GF2, level 13.7, damaged specimen, partially exfoliated, x 6.1; **V.** CPC XXXXX, from GF2, level 13.7, x 6.2; **W.** CPC XXXXX, from GF1, level 49, x 7.1; **X.** CPC XXXXX, from GF1, level 49, small specimen, x 11.7.

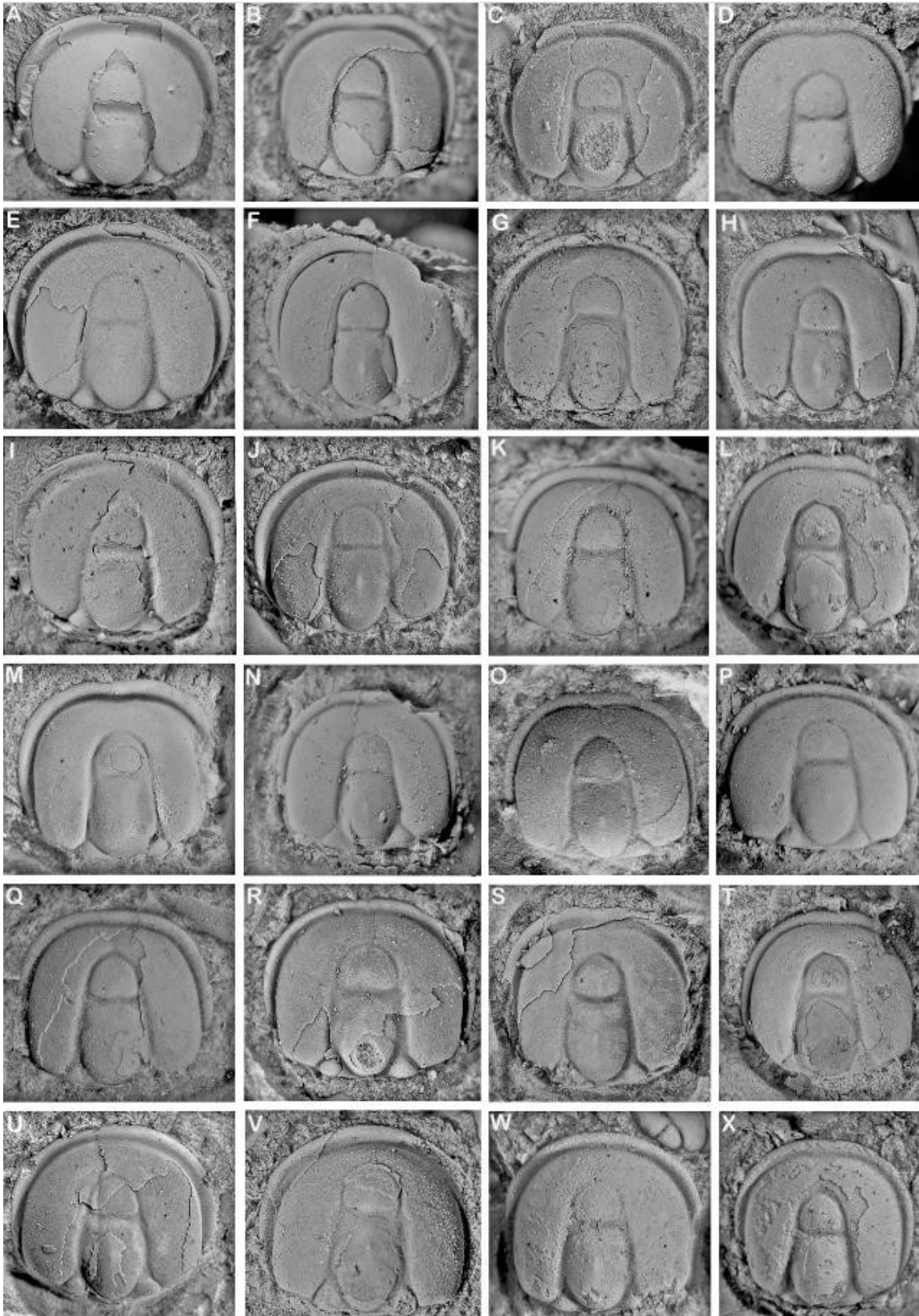


Figure 3-15. *Euagnostus interstrictus*

Figure 3-16. *Euagnostus interstrictus* pygidia: **A.** CPC XXXXX, from GF2, level 10, small specimen with wide border and narrower axis, x 13.7; **B.** CPC XXXXX, from GF2, level 12.2, x 4.7; **C.** CPC XXXXX, from GF1, level 59.7, x 6.9; **D.** CPC XXXXX, from GF1, level 53.3, x 8.3; **E.** CPC XXXXX, from GF1, level 53.3, x 6.4; **F.** CPC XXXXX, from GF1, level 53.3, small specimen with wide border and narrower axis, x 11.8; **G.** CPC XXXXX, from GF2, level 6, x 7.3; **H.** CPC XXXXX, from GF1, level 53.3, x 8.9; **I.** CPC XXXXX, from GF1, level 59.7, x 6.6; **J.** CPC XXXXX, from GF2, level 12.2, x 11.2; **K.** CPC XXXXX, from GF1, level 53.3, x 8.0; **L.** CPC XXXXX, from GF1, level 41.3, showing wide border but wide axis, x 9.2; **M.** CPC XXXXX, from GF2, level 13.7, x 6.0; **N.** CPC XXXXX, from GF1, level 59.7, x 7.6; **O.** CPC XXXXX, from GF2, level 13.7, x 6.4; **P.** CPC XXXXX, from GF2, level 13.7, x 7.7; **Q.** CPC XXXXX, from GF1, level 49, small specimen with wide border and narrower axis, x 15.2; **R.** CPC XXXXX, from GF1, level 49, x 6.9; **S.** CPC XXXXX, from GF2, level 13.7, x 6.3; **T.** CPC XXXXX, from GF2, level 10, x 9.4; **U.** CPC XXXXX, from GF2, level 13.7, x 5.9; **V.** CPC XXXXX, from GF2, level 13.7, x 5.5; **W.** CPC XXXXX, from GF2, level 12.2, x 6.0; **X.** CPC XXXXX, from GF1, level 59.7, x 7.6

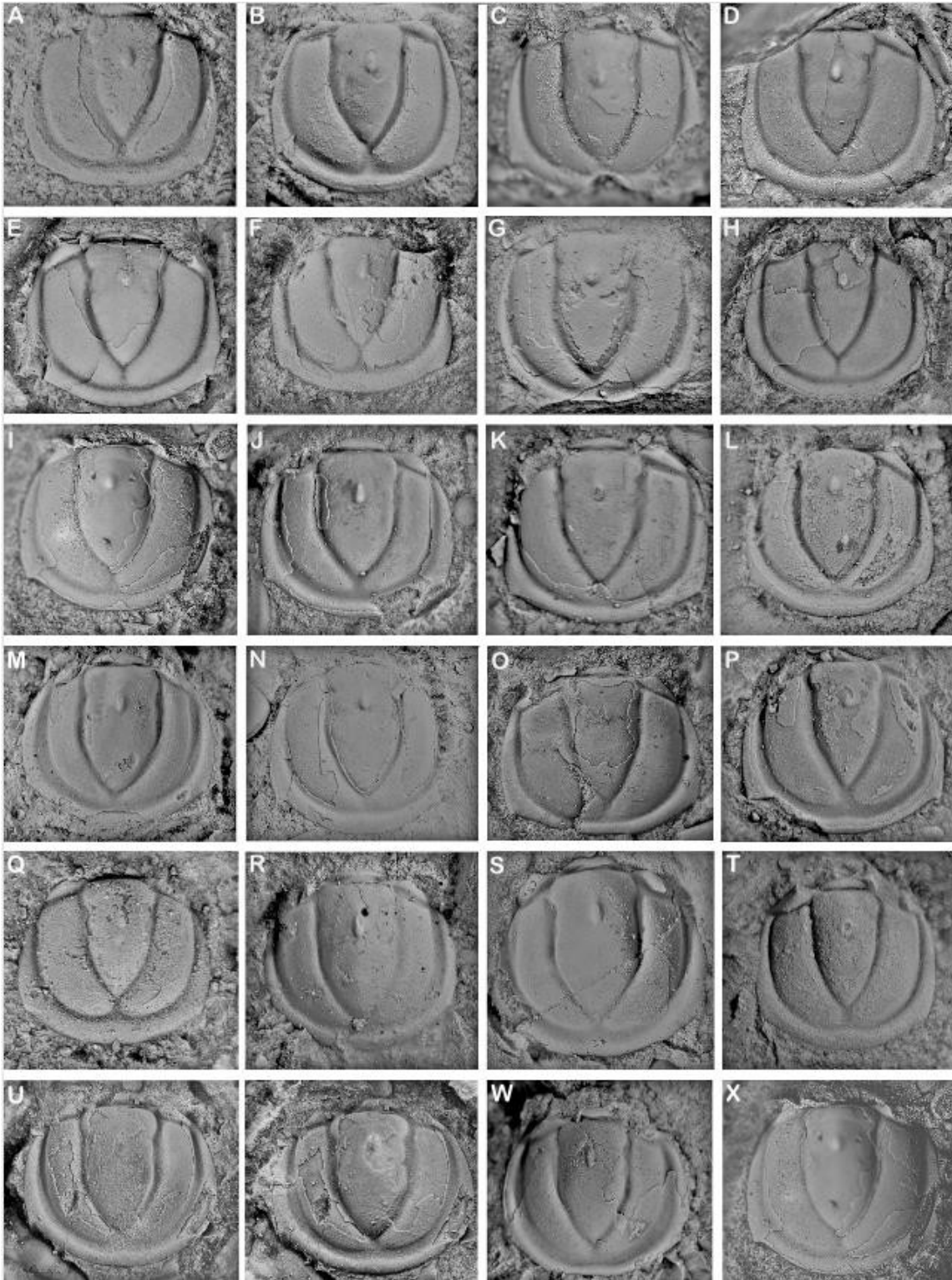


Figure 3-16. *Euagnostus interstrictus*

DORYAGNOSTINAE Shergold *et al.*, 1990.

Rhodotypiscus Öpik, 1979

Type species. *Rhodotypiscus nasonis* Öpik, 1979 (p. 79, pl. 16, figs 1–5)

Diagnosis. See Laurie (2004, p. 242).

Remarks. Robison (1994) and Peng and Robison (2000) synonymized *Rhodotypiscus* Öpik, 1979 with *Doryagnostus* Kobayashi, 1939, but Laurie (2004) retained *Rhodotypiscus* based on a more posteriorly located glabellar node, a weak preglabellar median furrow and a posteriorly inflated glabella. Jago and Cooper (2007) followed the synonymy of Robison (1994) and Peng and Robison (2000), without elaborating on their reasons. The diagnosis of family Doryagnostidae (*sensu* Shergold and Laurie, 1997) includes forms with a variably developed preglabellar median furrow and a glabellar node level with F1 furrows, but the type species of *Doryagnostus*, *D. incertus* (Brøgger, 1878) has a more anteriorly located glabellar node, a well developed preglabellar median furrow and a tapering, uninflated glabella. Laurie (2004) included *R. vinicensis* Šnadjr (1957) and *R. gaspensis* Rasetti (1948) in *Rhodotypiscus* as they have a parallel-sided, inflated glabella with a posteriorly placed glabellar node and the lack of the well-developed preglabellar median furrow is also highly distinctive of *Rhodotypiscus*. The Gowers Formation specimens are similar to those of *R. vinicensis* from Utah (Robison, 1978) in the shape of the glabella, but the majority of Robison's (1978) specimens have a defined continuous furrow, even if weak, with the exception of two specimens (see Robison 1978, pl. 1, fig. 6, pl. 2, fig. 9). None of the Gowers specimens show more than a very weak preglabellar median furrow and are hence most like those illustrated by Öpik (1979), in addition to those from Reilly Ridge, Antarctica (Jago and Cooper, 2007).

3.4.8. *Rhodotypiscus nasonis* Öpik, 1979 (Fig. 3-17A-S, Fig.3-18A-P)

1979 *Rhodotypiscus nasonis*; Öpik, p. 79, pl. 16, figs 1–5; pl. 59, fig. 1; text-fig. 23.

2004 ?*Rhodotypiscus* sp., Laurie, fig. 21I, p. 243

2006 ?*Rhodotypiscus* sp., Laurie, fig. 23, p. 151

Material. CPCXXRN1-49; 23 cephalata, 16 pygidia, GF1: 11.2–53.3, GF2: 1.2–17.6; *T. gibbus* Zone.

Emended diagnosis. *Rhodotypiscus* with broad, parallel-sided glabella, large semi-ovate anteroglabella, posteroglabella tumid at rear with median node situated level with, or slightly in front of, F1; F2 well developed. Pygidium with small border spines. Posteroaxis lanceolate to slightly ogival, median postaxial furrow usually present.

Description. Moderate to large size, with both cephalon and pygidium reaching about 5.5mm in length. Cephalon subrectangular, length 87–100% of width (n = 20); margin curves anterolaterally. Cephalic lateral border straight in holaspides but may be more rounded in juveniles (see Fig. 17J); cephalic border of medium width, roll-like; border furrow narrow to moderate in width, usually widening slightly at the mid-anterior of the acrolobe forming a deltoid depression; anterior acrolobe straight or slightly retral or emarginate; preglabellar furrow absent or weakly developed and very short; glabellar length 59–72% of cephalon length (n = 20); large semiovate anterior lobe with well- rounded front, 33–40% (n = 20) of glabellar length; posterior lobe with strongly inflated glabellar culmination, with F2 well developed and F1 weak; F3 straight or very slightly curved backwards; glabellar node level with or a short distance in front of F1. Basal lobes equilaterally triangular with an elongated anterior.

Thorax unknown.

Pygidium quadrate, length 94–100% of width (n =11); moderately convex with very small posterolateral spines; border of moderate width, flattened; border furrow about half as wide as border (sag.), sometimes with a small forward kink where it meets median postaxial furrow; postaxial median furrow usually present, narrow and reasonably long; axis length 69–78 % (n = 12) of pygidial length with a width of 30– 38% of pygidial width; F1 and F2 largely effaced, developed as slight indentations in sides of axis; M1 broad (tr.); M2 slightly constricted; posteroaxis ogival, occupying 45– 65% of axis length (n =10), posterior extremity usually pointed, maximum width behind F2. Axial node medium-sized, terminating to a short point. Small secondary node sometimes present, about two-thirds of distance between F2 and axistermination.

Figure 3-17. *Rhodotypiscus nasonis*: **A.** matching cephalon and pygidium, CPC XXXXX, from GF1, level 53.3, broken posteroglabella and pygidial axis, x ca.7.5; **B – S** are cephalata: **B.** CPC XXXXX, from GF2, level 12.2, small specimen showing wide border furrow, x 9.5; **C.** CPC XXXXX, from GF2, level 10, x 9.2; **D.** CPC XXXXX, from GF1, level 10, x 11.1; **E.** CPC XXXXX, from GF1, level 34.6, x 9.0; **F.** CPC XXXXX, from GF1, level 34.6, showing straight anterior, x 7.7; **G.** CPC XXXXX, from GF2, level 12.2, x 8.0; **H.** CPC XXXXX, from GF1, level 34.6, x 7.2; **I.** CPC XXXXX, from GF2, level 5.3, broken specimen, x 7.6; **J.** CPC XXXXX, from GF1, level 49, x 6.7; **K.** CPC XXXXX, from GF1, level 53.3, x 8.1; **L.** CPC XXXXX, from GF2, level 5.3, broken specimen, x 7.4; **M.** CPC XXXXX, from GF1, level 53.3, slightly distorted specimen, x 6.9; **N.** CPC XXXXX, from GF2, level 1 3.7, broken specimen, x 7.3; **O.** CPC XXXXX, from GF1, level 46.9, x 7.1; **P.** CPC XXXXX, from GF2, level 3.6, x 6.8; **Q.** CPC XXXXX, from GF1, level 46.9, x 6.4;

R. CPC XXXXX, from GF1, level 53.3, x 6.8; **S.** CPC XXXXX, from GF2, level 12.2, small specimen showing wide border furrow, x 8.5.

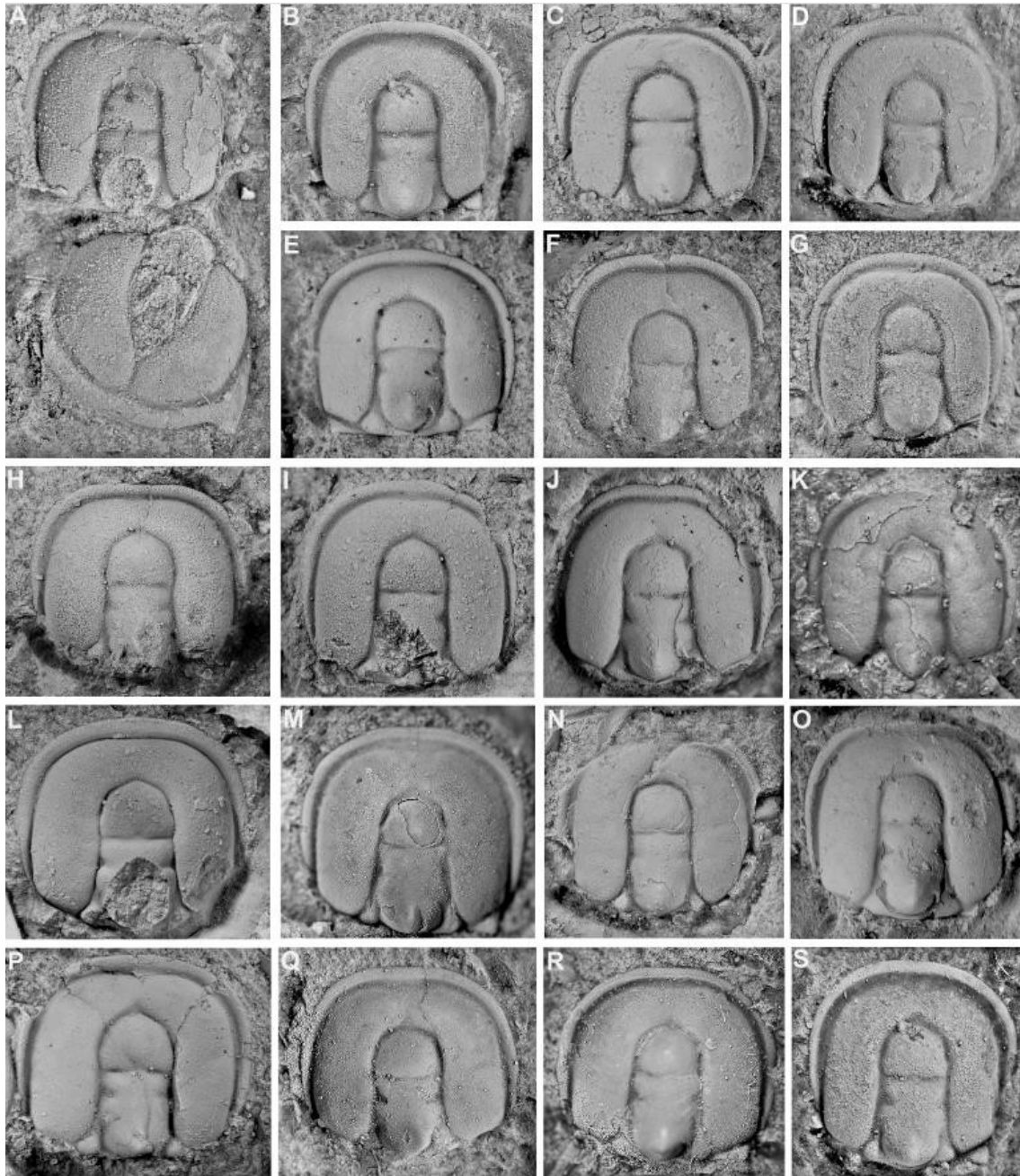


Figure 3-17. *Rhodotypiscus nasonis*

Figure 3-18. *Rhodotypiscus nasonis* pygidia: **A.** CPC XXXXX, from GF2, level 13.7, x 7.1; **B.** CPC XXXXX, from GF2, level 12.2, x 9.4; **C.** CPC XXXXX, from GF1, level 53.3, x 6.5; **D.** CPC XXXXX, from GF1, level 49, lacking a postaxial median furrow, x 5.7; **E.** CPC XXXXX, from GF1, level 53.3, 10.3; **F.** CPC XXXXX, from GF1, level 34.6, small specimen with narrower axis, x 10.7; **G.** CPC XXXXX, from GF1, level 46.9, x 7.8; **H.** CPC XXXXX, from GF1, level 41.3, x 7.7; **I.** CPC XXXXX, from GF1, level 13.7, lacking a postaxial median furrow, x 8.2; **J.** CPC XXXXX, from GF1, level 41.3, x 13.2; **K.** CPC XXXXX, from GF1, level 49, x 7.1; **L.** CPC XXXXX, from GF1, level 34.6, x 7.7; **M.** CPC XXXXX, from GF1, level 46.9, x 8.2; **N.** CPC XXXXX, from GF1, level 53.3, x 8.1; **O.** CPC XXXXX, from GF1, level 41.3, x 7.4; **P.** CPC XXXXX, from GF2, level 12.2, x 8.1.

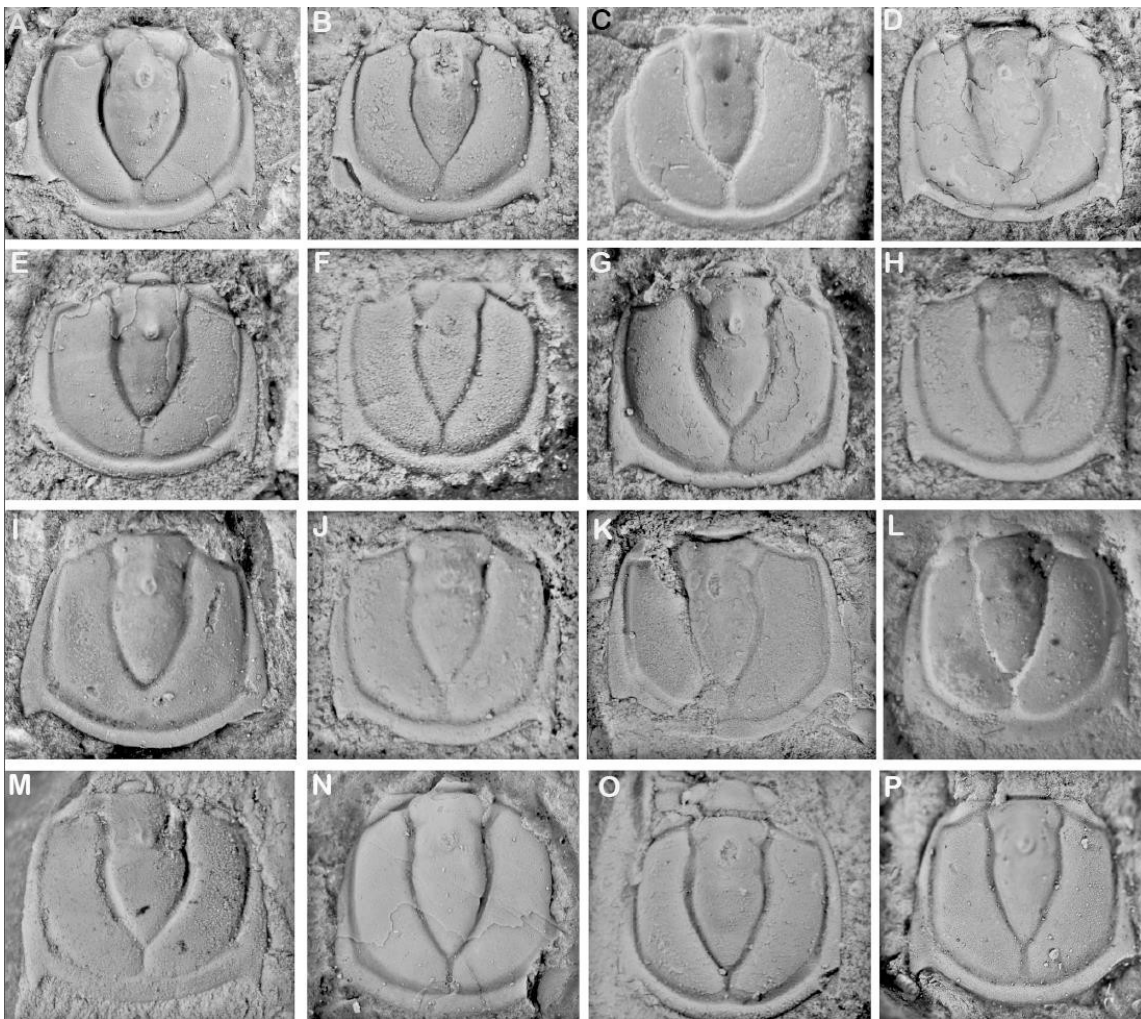


Figure 3-18. *Rhodotypiscus nasonis*

Remarks. *Rhodotypiscus nasonis* specimens are common in the Gowers Formation. They conform well to the description given by Öpik (1979), which is based on abundant specimens from localities in the Currant Bush Limestone, the Gowers Formation, Inca Formation and Age Creek Formation of the Georgina Basin. However, abundant Gowers specimens show variability in the curvature of the anterior cephalic border, with the smaller specimens tending to a more rounded anterior border. The weak median preglabellar furrow is quite similar in most specimens although somewhat less developed in Fig. 3-17F which is a small specimen. Also noticeable is the change in shape of the glabellar posterior lobe with growth, with small specimens having a raised and pointed culmination (see Fig.3-17K), developing into a broader, strongly inflated culmination. The pygidia show morphological variation in the width of the posteroaxis and the development of the postglabellar furrow.

Family PERONOPSIDAE Westergård, 1936

Peronopsis Hawle and Corda, 1847

Type species: *Peronopsis integer* Beyrich, 1845, from the *Paradoxides gracilis* Zone of Czech Republic (Bohemia); by monotypy.

Diagnosis. See Robison (1994, p. 42; 1995, p. 302).

Remarks. Many peronopsoid (*sensu stricto*) species exhibit very diverse morphologies (Weidner and Nielsen, 2013) and the more restricted definition of *Peronopsis* advocated by Shergold and Laurie (1997) and Laurie (2004) is followed here.

3.4.9. *Peronopsis amplaxis* Robison 1982 (Fig. 3-19A-T)

1982 *Peronopsis amplaxis* Robison, p. 150; pl. 5, figs 1–12.

1987 *Peronopsis amplaxis* Robison; Shah and Sudan, p. 52; Pl. I, b,h; Fig. 1, f,k.

1996 *Peronopsis amplaxis* Robison; Sahni and Sudan, p. 654, Pl. 2, g–q.

Diagnosis. See Robison (1982, p. 150).

Material. XXPA1-20; 13 cephalata, 7 pygidia from GF1: 28.3–59.7; *T. gibbus* Zone.

Description. Small agnostid, with both cephalon and pygidium reaching about 3.5mm in length; nonscrobiculate; cephalon subcircular, with length approximately equal to width; moderately convex; glabella 63–79% (n = 12) of cephalic length, width at F3 greater than width of adjacent genae, tapers slightly, broadly to bluntly rounded at anterior end. Median preglabellar furrow absent; anteroglabella semiovate, width 64–82% of length (n = 12). Posteroglabella larger and rounded at rear; median node very faint, a short distance behind F2. Border narrow; border furrow narrow and shallow, narrowing posterolaterally. Basal lobes small, subtriangular.

Thorax unknown.

Pygidium subcircular with length 69–85% of width (n = 12), slightly less convex than cephalon. Axis broad, ca. 44% of pygidial width; axis length 76–81 % of pygidial length (n = 4). Axis only slightly constricted at M2, maximum width about midlength; posteroaxis broadly ogival, strongly convex, generally ending short of posterior border furrow by distance about equal to width (sag.); F1 and F2 poorly defined or absent. Median axial node elongate and weak. Postaxial median furrow weakly developed. Border wide and flat, widest posteriorly, narrowing anterolaterally. Lacks marginal spines. Axial node slightly anterior of mid-length. A weakly developed transverse depression at about midlength on some specimens (Fig. 3-19Q, S, T)

Remarks. *Peronopsis amplaxis* is a distinctive small agnostid with a wide cephalic axis and a wide pygidial border. The Gowers specimens closely match those from the lower *T. gibbus* Zone of Utah and Nevada (Robison, 1982). Robison (1984) also reports *P. amplaxis* from North Greenland but does not provide illustrations or a description. The illustrations of the Himalayan specimens are too poor to be certain of their identity.

Figure 3-19. *Peronopsis amplaxis*: A – M are cephalia: **A.** CPC XXXXX, from GF1, 46.9, x 15.7; **B.** CPC XXXXX, from GF1, level 53.3, partially exfoliated, x 15.7; **C.** CPC XXXXX, from GF1, level 53.3, x 13.2; **D.** CPC XXXXX, from GF2, level 12.2, x 13.9; **E.** CPC XXXXX, from GF1, level 49, x 21.9; **F.** CPC XXXXX, from GF2, level 13.7, x 16.3; **G.** CPC XXXXX, from GF2, level 13.7, broken anterolaterally, x 15.2; **H.** CPC XXXXX, from GF1, level 53.3, x 20.6; **I.** CPC XXXXX, from GF1, level 46.9, x 15.2; **J.** CPC XXXXX, from GF2, level 13.7, x 9.7; **K.** CPC XXXXX, from GF1, level 53.3, x 14.0; **L.** CPC XXXXX, from GF2, level 13.7, x 25.7; **M.** CPC XXXXX, from GF1, level 59.7, broken anterior, x 22.2; **N – T** are pygidia: **N.** CPC XXXXX, from GF1, level 41.3, with partial thoracic segment, x 13.9; **O.** CPC XXXXX, from GF1, level 53.3, x 14.3; **P.** CPC XXXXX, from GF1, level 53.3, x 17.5; **Q.** CPC XXXXX, from GF2, level 17.6, partially exfoliated specimen, x 13.0; **R.** CPC XXXXX, from GF1, level 49, showing wide axis, x 14.7; **S.** CPC XXXXX, from GF2, level 13.7, x 11.1; **T.** CPC XXXXX, from GF2, level 20.8, x 7.9

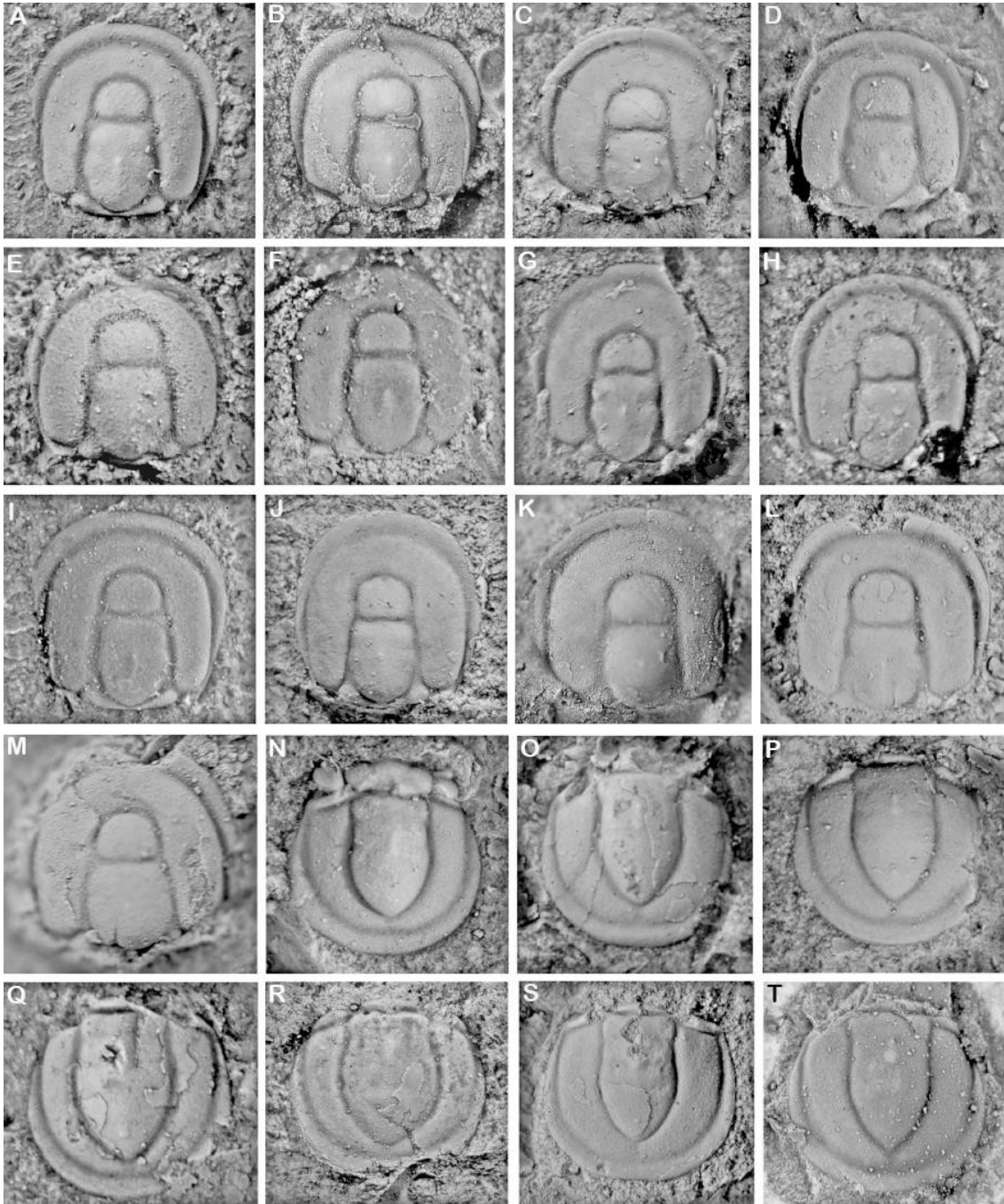


Figure 3-19. *Peronopsis amplaxis*

Family DIPLAGNOSTIDAE Whitehouse, 1936

Subfamily DIPLAGNOSTINAE Whitehouse, 1936 *Acadagnostus* Kobayashi, 1939

Type species. *Agnostus acadicus* Hartt in Dawson, 1868, p. 655 [= *Agnostus fallax* Linnarsson, 1869, p. 81, pl. 2, figs 54-55].

Remarks. The interpretation of this genus has proved difficult because its type species, *Agnostus acadicus*, is based on tectonically distorted and mixed syntype material (Robison 1995), including a pygidium of *Hypagnostus parvifrons*. Robison (1995) revised *Acadagnostus acadicus* (Hartt) and considered it to be a senior synonym of *A. fallax* Linnarsson, 1869. Laurie (1990) assigned *A. fallax* (as type species of *Axagnostus* Laurie) to the Diplagnostidae due to its cephalon having large triangular basal lobes, a transverse anterior glabellar lobe and a posteriorly positioned glabellar node, and a pygidium with an unrestricted and relatively short axis with a subtriangular posterior lobe. Naimark (2012) presents the most recent treatment of *Acadagnostus*, supporting its position in the Diplagnostidae. Her concept is supported here with some additional information.

Emended diagnosis. Cephalon round to semi-quadrate, preglabellar furrow absent or incomplete; border narrow, border furrow wide, narrower in some juvenile specimens; lateral furrows of posterior lobe of glabella in shape of pits or narrowing of dorsal furrow, transglabellar furrow straight, sometimes curved slightly posteriorly; median node located in centre of, or slightly below centre of, posterior lobe. Pygidium subquadrate, border flat or rolled, sometimes posteriorly widened and with weak bifurcation, bispinose; border furrow wide; axis with parallel lateral sides or conical, constriction at level of second segment absent or slight, transaxial furrows absent to well-developed; segments marked by relief of

axis, median node large; postaxial furrow usually present or at least indicated but usually short.

3.4.10. *Acadagnostus rakuroensis* Kobayashi, 1935 (Fig.3-20 A-Q, Fig. 3-21A-U)

1978 *Baltagnostus australis* (Robison), Jell & Robison, p. 5, Pl. 1, figs 3, 5-7, 9-11.

1987 *Baltagnostus rakuroensis* (Kobayashi); Zhang and Jell, p. 39. cum. syn.

1987 *Baltagnostus rakuroensis* (Kobayashi); Zhang and Jell, p. 39, Pl. 1, figs 1-15; Pl. 2, figs 1-6, 8; Pl. 3, fig. 10.

2006 *Acadagnostus* aff. *acadicus* Hartt in Dawson, 1868, Laurie, 2006, Fig. 24.

2012 '*Acadagnostus*' *australis* (Robison in Jell and Robison 1978) Laurie, Fig. 3C, D, G, H.

Material. CPCAR1-AR35, 3 adult complete specimens, ten adult cephalae, eight adult pygidia, seven complete juvenile specimens, eight juvenile cephalae, two juvenile pygidia, from GF1: 11.2 to 59.7, GF2: 1.2 to 20.8; *T. gibbus* to lower *A. atavus* Zones.

Diagnosis. Rounded to subquadrate glabella with partial preglabellar median furrow; rounded to subquadrate pygidium with large axial node, conical posteroaxis, bispinose, posteriorly located secondary node.

Description. Cephalon subrectangular to rounded in both juvenile and adult specimens, av. glabellar width: length = 111%, in juvenile specimens (n = 8), and in adults (n = 8); moderately convex, nonscrobiculate, border narrow, roll-like, border furrow narrow in juveniles, becoming very wide in adults; a very short, incomplete preglabellar median furrow is usually present and variably developed; glabella 65–73% (av. = 69, n = 14) as long as cephalon in adults and juveniles, with anterior lobe well developed, occupying 30–36%

(av. = 33, n = 14) of glabellar length in both adults and juveniles, semiovate. F3 clearly incised, straight or very slightly curved posteromedially; posterior glabellar lobe parallel-sided then tapering to a rounded culmination, sometimes more tapered, in both juveniles and adults; F2 non- or weakly developed in juveniles, becoming well- developed in adults; F1 usually developed as slight indentations at anterior extremities of basal lobes in adults, non-existent in juveniles; glabellar node situated anteriorly of mid-posteroglabella length, varying slightly in position; glabella approximately equal in width to adjacent genae (measured at position of transglabellar furrow) but genae slightly wider in adult specimens; anterior lobe 30–35% glabellar length; and tiny median ridge just above cephalic recess. Lateral sides of acrolobes slightly tapered toward anterior.

Thorax non-spinose. with elements well-defined; anterior segment with well-developed pleural furrows separating a triangular posterior pleural band from an ovately bulbous anterior pleural band; axial lobe with clearly developed lateral lobes and broad (tr.) trapeziform median lobe with a large median ovate tubercle; posterior segment with well-developed pleural furrows separating narrow anterior pleural band from laterally tapering posterior pleural band; axial lobe with weakly defined lateral lobes and broad trapeziform median lobe.

Pygidium subrectangular, width: length greater in juveniles, = 71–85% (av. = 77, n = 5), 67–74 (av. = 70, n = 6) in adults; av. length of adult pygidium = 4.2 mm, juvenile = 2.3 mm; av. width of adult pygidium = 5.9 mm, of juvenile = 2.5 mm; pygidial axis wide, in juveniles axis width is 71–85% of pygidial width, (av. = 77, n = 5), decreasing in adults to 67–74% of pygidial width (n = 6); pygidial axis length is 67–77 % (n = 5) of pygidial length in juveniles and increases to 74–84% in adults (n = 7). Lateral margins usually becoming more rounded in adults; moderately convex, with posterolateral spines which become smaller in adults; flat

border narrowing laterally and widening posteriorly in both juvenile and adult specimens; border furrow moderately wide in juveniles, growing to very wide in adult specimens, with greatest width anterior of the posterolateral spines; postaxial median furrow is a variable character in both juveniles and adults, from non-existent (juv.- Fig 3-20F; ad.- Fig. 3-21J) to weakly incised (juv.- Fig. 20E; ad.- Fig. 21G) to reaching the border (Figs 3-20G, P; ad. - Fig.3-21 H). Posteroaxis tapers more to a point in adults. M1 similar in proportion in juveniles and adults; F1 well defined in both juveniles and adults; M2 not constricted in juveniles, constricted in adults; F2 well defined in adults, absent in juveniles. Large axial node, ovate in juveniles, ovate but becoming longer in adult specimens.

Remarks. The validity of this species has been controversial (see Naimark, 2012), but the abundant specimens from the Gowens Formation now shed light on its definition. The species was referred to *Baltagnostus* by Zhang and Jell (1987), which is defined as having a zonate border (Laurie *et al.*, 1990; Shergold and Laurie, 1997). However, their illustrated specimens do not show a zonate border and thus cannot be assigned to *Baltagnostus*, as recently acknowledged by Naimark (2012), who assigned both *B. rakuroensis* Kobayashi and *B. australis* Robison to *Acadagnostus*. Laurie (2014) illustrated three specimens which are clearly conspecific with specimens referred to as *B. australis* Robison (Laurie, 2014, Fig. 3C, D, G, H) but acknowledged that they cannot belong to *Baltagnostus* due to their lack of zonation of the pygidium. Laurie stated that they are perhaps most like *Acadagnostus* due to their large simple basal lobes and their overall pygidial morphology. Due to the abundance of specimens, it is here demonstrated that this species has a high variability, both morphologically and ontogenetically, and that the few specimens of *B. damesi* and *B. australis* illustrated by Jell and Robison (1978), as well as those of Zhang and Jell (1987),

fit well within the determined limits of intraspecific variation. The specimens here are assigned to *Acadagnostus rakuroensis* (Kobayashi, 1935).

Kobayashi (1962) noted the similarity of *B. damesi* and *B. rakuroensis* but distinguished them on the basis of the complete preglabellar median furrow that was erroneously added to illustrations of *B. damesi* by Endo and Resser (1937). Zhang and Jell (1987) synonymized *B. damesi* with *B. rakuroensis* but separated *B. australis* on the basis of a narrow axis, presumably the cephalic axis as stated originally in Jell and Robison (1978). Jell and Robison's (1978) specimens of *B. australis* are juveniles and as such have a narrower posteroaxis than larger specimens. Jell and Robison (1978) also discussed the similarity of *B. damesi* and *B. rakuroensis* but retained *B. damesi* as a separate species due to a lack of material. The specimens of Zhang and Jell (1987) represent both juvenile and adult forms and as such record some ontogenetic variation in characters such as the length of the pygidial axis.

Figure 3-20. *Acadagnostus rakuroensis* (juvenile): A – G are entire specimens: **A.** CPC XXXXX, from GF1, level 41.3, x 9.0; **B.** CPC XXXXX, from GF1, level 11.2, flattened specimen, x 11.4; **C.** CPC XXXXX, from GF1, level 11.2, slightly flattened specimen, x 9.8; **D.** CPC XXXXX, from GF1, level 11.2, x 8.6; **E.** CPC XXXXX, from GF1, level 22.5, x 10.0; **F.** CPC XXXXX, from GF1, level 11.2, x 15; **G.** CPC XXXXX, from GF1, level 11.2, x 10.8; **H – O** are cephalae: **H.** CPC XXXXX, from GF2, level 13.7, x 11.5; **I.** CPC XXXXX, from GF2, level 17.6, very small specimen, x 18.3; **J.** CPC XXXXX, from GF1, level 7, x 7.5; **K.** CPC XXXXX, from GF1, level 11.2, small flattened specimen with cracks, x 15.2; **L.** CPC XXXXX, from GF1, level 59.7, small specimen, x16.1; **M.** CPC XXXXX, from GF1, level 59.7, x 12.5; **N.** CPC XXXXX, from GF1, level 14, x 8.9; **O.** CPC XXXXX,

from GF2, level 7, x 10.3; **P.** CPC XXXXX, from GF1, level 11.2, pygidium, x 9.4; **Q.** CPC XXXXX, from GF1, level 22.5, slightly flattened pygidium with cracks, x 8.3 .

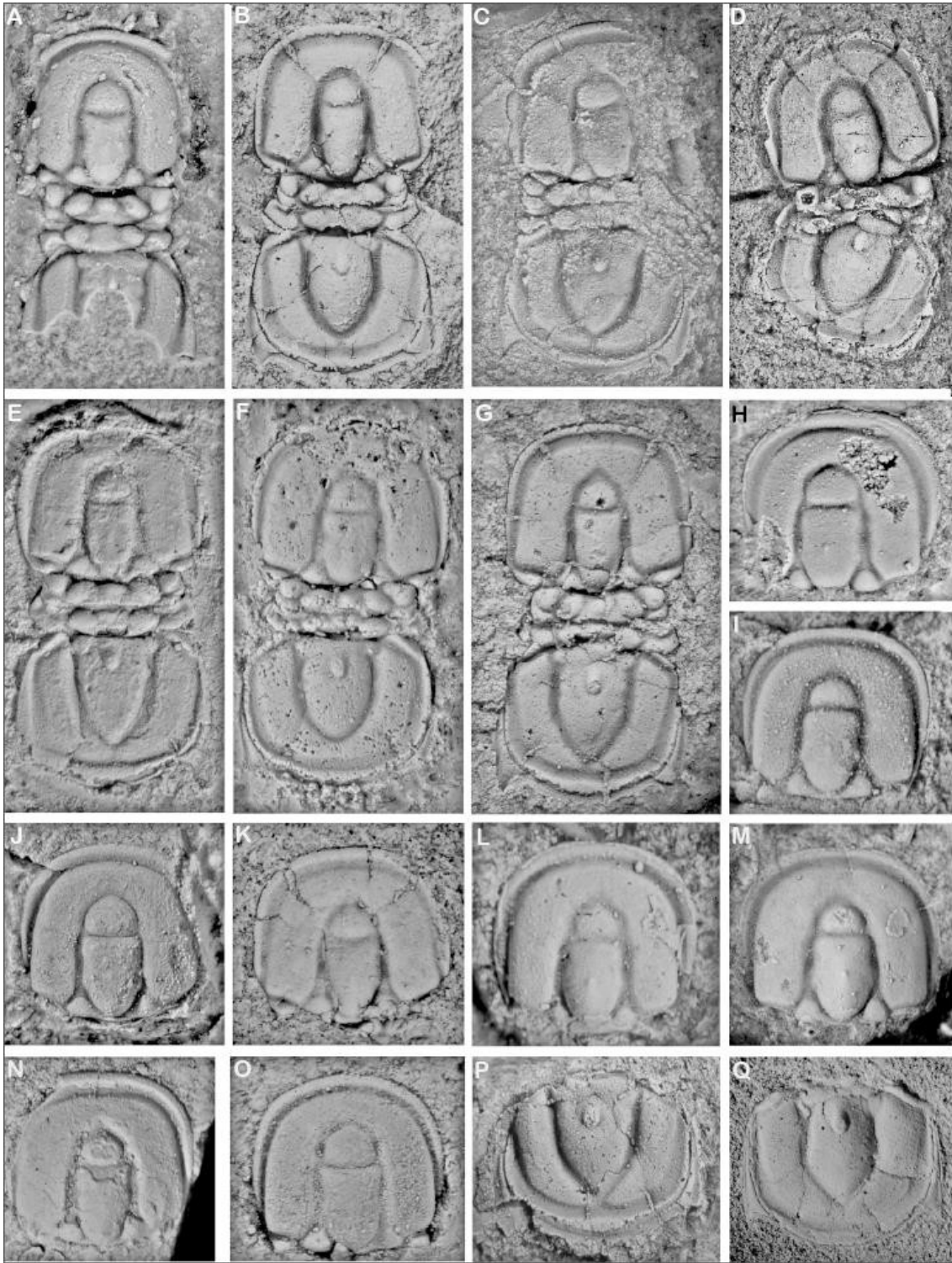


Figure 3-20. *Acadagnostus rakuroensis* (juvenile)

Figure 3-21. *Acadagnostus rakuroensis* (adult): **A.** CPC XXXXX, from GF2, level 8.3, cephalon, pygidium and part thoracic segment, showing pygidial postaxial median furrow, x 7.1; **B.** CPC XXXXX, from GF2, level 17.3, cephalon, pygidium and one thoracic segment, x 5.6; **C.** CPC XXXXX, from GF1, level 41.3, cephalon, thorax and broken pygidium, x 8.3; **D.** CPC XXXXX, from GF1, level 39.5, cephalon, x 7.3. **E.** CPC XXXXX, from GF2, level 12.2, cephalon, x 8.1; **F.** CPC XXXXX, from GF2, level 8.3, cephalon with straight anterior and well developed F1, x 4.6; **G.** CPC XXXXX, from GF1, level 53.3, cephalon showing well developed F1, x 7.1; **H.** CPC XXXXX, from GF2, level 13.7, cephalon with rounded outline and well developed F1, x 5.6; **I.** CPC XXXXX, from GF1, level 49, cracked cephalon with wide border furrow, x 5.9; **J.** CPC XXXXX, from GF2, level 13.7, cephalon showing wide border furrow and well developed border furrow, x 3.5; **K.** CPC XXXXX, from GF1, level 53.3, cephalon showing well developed F1, x 7.1; **L.** CPC XXXXX, from GF2, level 13.7, cephalon with rounded outline, x 5.7; **M.** CPC XXXXX, from GF1, level 53.3, x 8.7; **N – U** are pygidia: **N.** CPC XXXXX, from GF2, level 1.2, showing wide border furrow, x 7.7; **O.** CPC XXXXX, from GF1, level 46.9, showing wide border furrow and well developed F1 and F2, x 5.9; **P.** CPC XXXXX, from GF2, level 12.2, showing well developed F1 and F2, x 5.5; **Q.** CPC XXXXX, from GF2, level 15.8, x 7.1; **R.** CPC XXXXX, from GF2, level 17.6, showing wide border furrow and well developed F1 and F2, x 5.1; **S.** CPC XXXXX, from GF2, level 12.2, showing wide border furrow and well developed F1 and F2, x 5.5; **T.** CPC XXXXX, from GF1, level 46.9, showing wide border furrow and well developed F1 and F2, x 6.2; **U.** CPC XXXXX, from GF2, level 15.8, showing well developed F1 and F2, x 6.8.

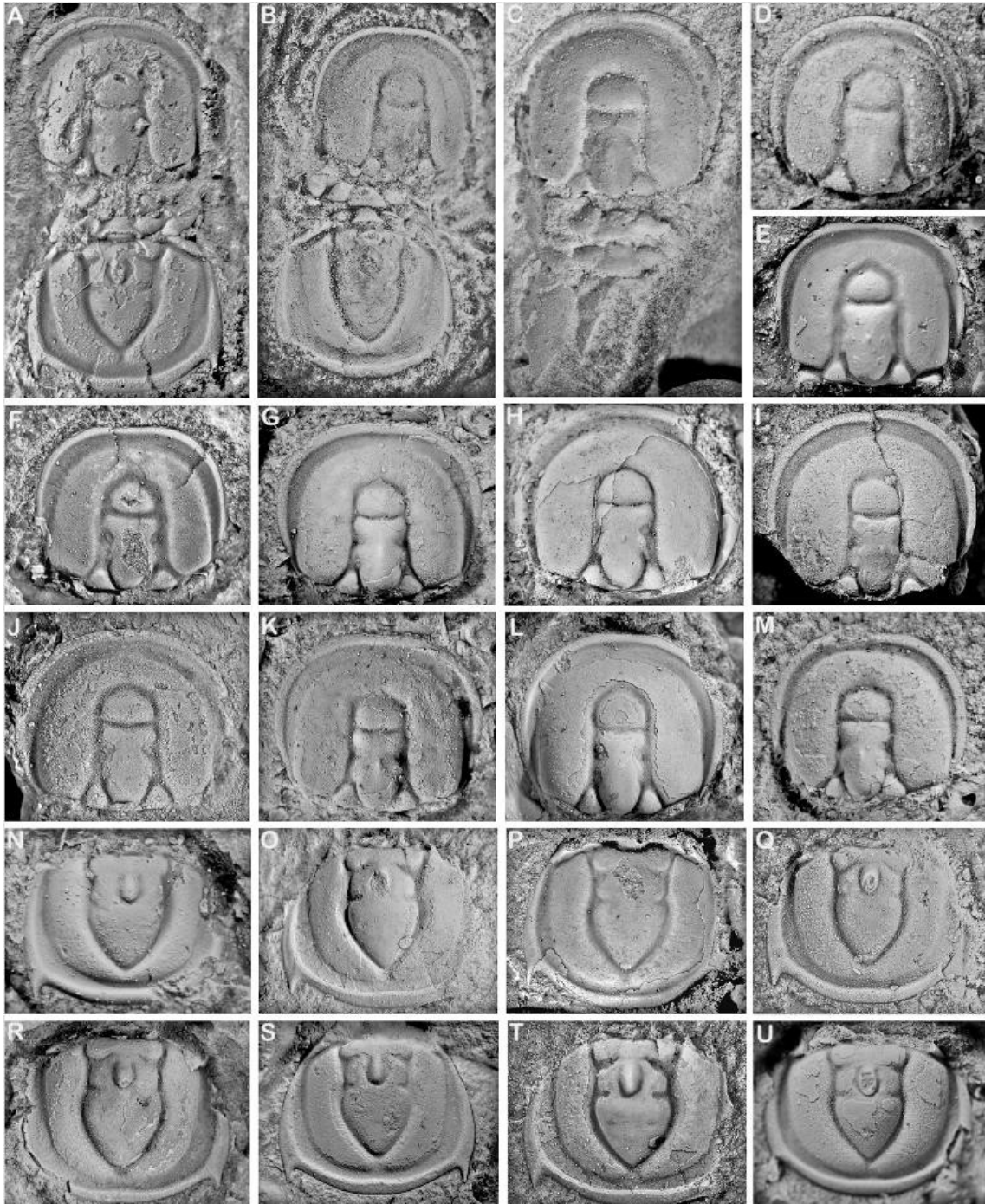


Figure 3-21. *Acadagnostus rakuroensis* (adult)

The variability of this species highlights the problems which arise when isolated specimens are used to construct new species and morphological and ontogenetic variation are not taken into account. The ontogenetic variation in this species occurs in characters such as the depth of furrows, general shape of the axes, and proportions in cephalic or pygidial dimensions. In adult specimens, F1 occurs as slight indentations and F2 are well-developed, while in juveniles, F1 are non-existent and F2 are weakly developed. The adult pygidium has a smaller width: length, a narrower axis, is longer and has slightly smaller spines and a much wider border furrow. The lateral pygidial margin also becomes more rounded with growth.

Order EODISCIDA Kobayashi, 1939

Superfamily EODISCOIDEA Raymond, 1913

Family EODISCIDAE Raymond, 1913

Pagetia Walcott, 1916

Type species. *Pagetia bootes* Walcott, 1916

Synonymy. See Jell (1975, p. 30).

Remarks. Jell (1975) undertook a review of the Eodiscoidea, analyzing material from Cambrian Series 3 of the Georgina Basin, Queensland and Northern Territory, and from western New South Wales.

3.4.11. *Pagetia thorntonensis* Jell 1975 (Fig. 3-22A-L)

1975 *Pagetia thorntonensis* Jell, p. 65–67, pl. 22, figs 1-10; pl. 27, figs 1–6; text-fig. 21a.

1975 *Pagetia whitehousei* Jell, p. 69–71, pl. 22, fig. 11; pl. 23, figs 1–16; text-fig. 21b.

Material. CPCXXPT1-12; eight cephalata, four pygidia from GF1: 53.3, GF2: 13.7–15.8; *T. gibbus* to lower *A. atavus* Zone.

Diagnosis: See Jell (1975, p. 65).

Remarks: Jell (1975) gave detailed descriptions of both *P. thorntonensis* and *P. whitehousei*, which were found together in the lowest 20 metres of the Currant Bush Limestone at locality QML128; this site most likely represents the Gowers Formation. However, there are some inconsistencies in the descriptions given by Jell (1975) of these two species. *P. thorntonensis* is described as having 12-18 scrobicules on the anterior border. This character should not be used to differentiate the two above species as the scrobicules are somewhat difficult to count on the photographs and as *P. whitehousei* is described as having 15 to 25 scrobicules which overlaps the number on *P. thorntonensis*, accuracy is needed. Secondly, Jell states that there are four axial rings then later that there are five axial rings on the pygidium of *P. whitehousei* (Jell 1975, p. 70), while the illustrations show four rings plus a terminal piece. *P. thorntonensis* also has four rings and a terminal piece. The Gowers specimens have four axial rings and a terminal piece. Jell states that *P. whitehousei* can be differentiated from *P. thorntonensis* by its lack of the punctate ornament, which appears on both the cephalon and pygidium. Two Gowers specimens have punctate cephalata which on closer examination appears to be due to be preservation related. Fig.3-22F is an exfoliated specimen showing punctation and Fig. 3-22G shows the punctate ornament only on the exfoliated section of the cephalon. No ornament appears on the other specimens. Photograph of *P. thorntonensis* (Jell 1975, Pl. 22, figs 2, 3, 7, 8, 10) show the punctae occur only on the exfoliated parts of the specimens.

Figure 3-22. *Pagetia thorntonensis*: A – H are cephalae in which the cephalic spine is broken off, except for specimen in K: **A.** CPC XXXXX, from GF2, level 13.7, x11.7; **B.** CPC XXXXX, from GF2, level 13.7, x 20.6; **C.** CPC XXXXX, from GF2, level 13.7, x 18.3; **D.** CPC XXXXX, from GF2, level 13.7, x 18.3; **E.** CPC XXXXX, from GF1, level 49, x 11.2; **F.** CPC XXXXX, from GF2, level 13.7, exfoliated specimen showing punctate ornament, x 17.5; **G.** CPC XXXXX, from GF2, level 13.7, x 20.0; **H.** CPC XXXXX, from GF2, level 13.7, mostly exfoliated specimen showing punctate ornament, with spine attached, x 13.5; I – L are pygidia in which the pygidial spine is broken off except for that of K: **I.** CPC XXXXX, from GF2, level 15.8, x 19.4; **J.** CPC XXXXX, from GF2, level 13.7, x 15.0; **K.** CPC XXXXX, from GF1, level 53.3, with spine intact, x 19.4; **L.** CPC XXXXX, from GF2, level 13.7, x 17.5.

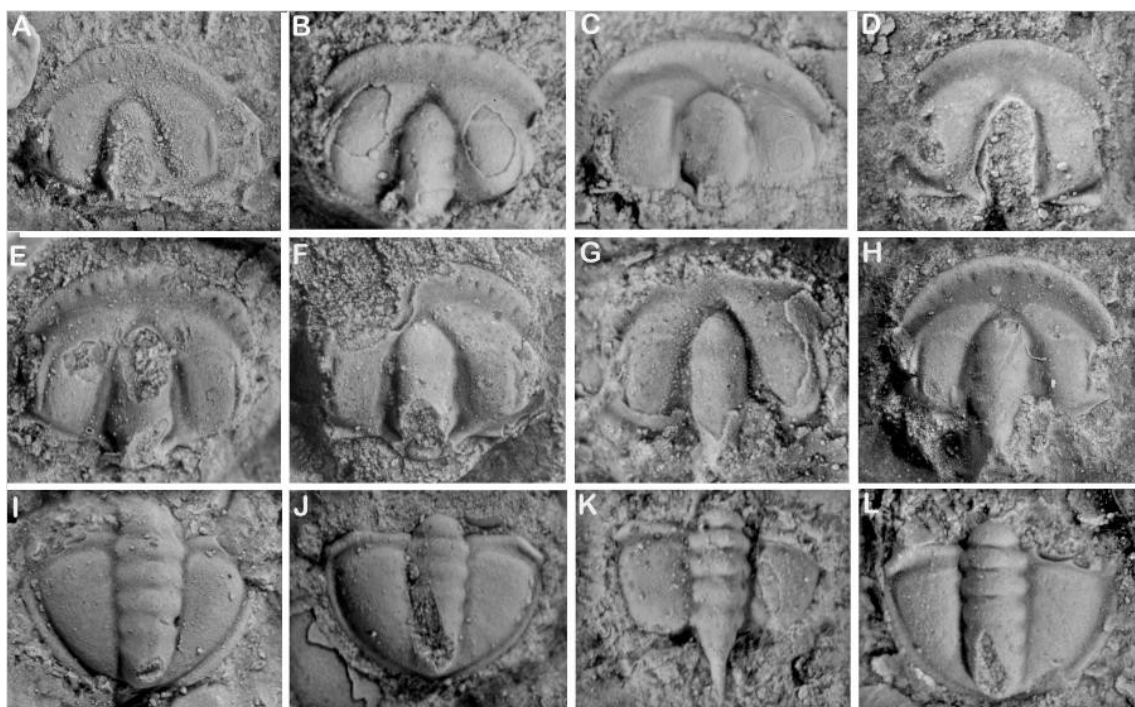


Figure 3-22. *Pagetia thorntonensis*

Family DOLICHOMETOPIDAE Walcott, 1916

Amphoton Lorenz, 1906

1982 *Horonastes* Öpik, p. 20.

2004 *Amphoton* Peng *et al.*, p. 54 (cum. syn.).

2004 *Amphoton* Lieberman, p. 11.

2007 *Amphoton* Kang and Choi, p. 285.

2015 *Amphoton* Smith *et al.*, p. 182.

Type species. *Amphoton steinmanni* Lorenz, 1906 (= *Dolichometopus deois* Walcott, 1905).

Remarks. For comprehensive discussions of the genus, see Zhang and Jell (1987, p. 62) and Peng *et al.* (2004, p. 54). Members of *Amphoton* from mainland Australia have close similarities to *Horonastes* Öpik, 1982. Smith *et al.* (2015) considered *Horonastes* to be a junior subjective synonym of *Amphoton*, after Lieberman (2004) suggested this synonymy based on the fact that many of Öpik's (1982) diagnostic characters of *Horonastes* are often found in species of *Amphoton*, including the type species (Zhang and Jell, 1987, for extensive illustration).

3.4.12. *Amphoton eminens* (Öpik, 1982) (Fig. 3-23A-P, Fig. 3-24A-H)

1982 *Honorastes eminens* Öpik, p. 21, Pl.4, figs 1-4, Pl. 5, figs 1-6, tect-fig. 6.

Material: 20 complete cephalae, 4 pygidia, 7 librigenae from GF1: 49—54.7; GF2: 13.7—20.8; *T. gibbus* to lower *A. atavus* Zones

Description: Largest cranidium 15.0 mm long (sag.), subquadrate with L: W = 101% (n=10) (excluding occipital spine), moderately convex; maximum width across posterior limbs of fixigenae; narrowest part of cranidium at S2. Anterior margin curved, posterior margins parallel except for occipital ring posterior margin which curves posteriorly.

Anterior branches of facial sutures diverge at 30° before they intersect the cranial margin; ϵ - ω diverge from one another at ca. 180° . Glabella almost quadrate, parallel-sided and convex, with maximum convexity across midwidth, lateral slopes gently curved; width: length = 57–70% (mean = 64, n = 14), occupying ca. 70% cranial length (excluding occipital spine), slightly expanding anterior of S3 with maximum width across anterolateral corners. Axial furrows narrow and relatively shallow. S1 deep and directed posteromedially, sometimes changing to a more posteriorly directed angle about halfway; S2 much less strongly defined, directed slightly posteromedially and shorter than S1; S3 very weakly defined and directed slightly forwards adaxially; S4 usually weakly defined or effaced, parallel to S3. Occipital ring of moderate width, narrowing abaxially, surmounted by a broad-based occipital spine; SO straight or curved very slightly backwards, shallow medially, moderately wide (sag. and exsag.). Preglabellar and preocular fields slope down to a very shallow, narrow border furrow which runs parallel to the anterior glabellar margin. Anterior border narrow (sag. and exsag.) and convex, border occupying 9% of cranial length (sag.). Palpebral lobe strongly curved, length (exsag.) ca. 50% of total cranial length (sag.), defined by a shallow to slightly wider, palpebral furrow which intercepts axial furrow at the level of S4. Palpebral area of fixigena convex, maximum width opposite S1 where it is 43–48% (n = 7) as wide as the adjacent glabella. Postocular field very short (exsag.) and strongly downsloping. Posterolateral projection of fixigena long, expanding abaxially.

Librigena up to 9.8 mm in length (exsag.), excluding genal spine. Lateral margins curved, posterior margin narrow (tr.). Librigenal field of very moderate convexity, trapeziform, occupying ca. 85% (n = 2) of librigenal width. Lateral and posterior borders narrow and border furrow shallow. Genal spine is triangular, flat and short.

Unknown no. segments in thorax.

Pygidium semi-elliptical in outline, length (sag.): width (tr.) = 53% (n = 4), moderately convex; axis strongly convex (tr.), tapering rearward, occupying 73% of pygidial length and 35% of pygidial width at the anterior margin (n = 4). Articulating half-ring poorly preserved. Two axial rings present, separated by narrow (sag.), deep inter-ring furrows which become progressively shallower medially (sag.) and posteriorly, central node on each axial ring. Terminal piece short. Axial furrows narrow and shallow. Pleural regions gently convex; three pleural furrows and three pair of fused delicate ridges forming interpleural partitions (Öpik, 1982); flat, wide pygidial border, marginal furrow shallow.

Prosopon smooth on majority of cranidium and pygidium, punctate on occipital lobe and middle of posterior part of glabella. Librigenal field usually with caecae, lateral border smooth.

Hypostome has a pair of prominent maculae (Fig. 3-23S, T).

Remarks: Öpik (1979) described this species in detail (as *Horonastes eminens*), based on specimens from locality M179 of the Currant Bush Limestone, which is possibly part of the Gowers Formation. Öpik detailed morphological differences based on abundant well-preserved specimens. The Gowers specimens fall within the variation range of the species shown by Öpik's specimens.

Figure 3-23. *Amphoton eminens*: A – N are cephalata: **A.** CPC XXXXX, from GF1, level 54.7, with cephalic spine, x 3.4; **B.** CPC XXXXX, from GF1, level 59.7, with cephalic spine, x 2.4; **C.** CPC XXXXX, from GF1, level 59.7, x 2.3; **D.** CPC XXXXX, from GF1, level 59.7, x 2.4; **E.** CPC XXXXX, from GF1, level 59.7, showing right lateral projection, x 4.2; **F.** CPC XXXXX, from GF1, level 59.7, x 4.2; **G.** CPC XXXXX, from GF1, level 59.7 (John Laurie Collection), x 4.7; **H.** CPC XXXXX, from GF1, level 59.7, x 4.3; **I.** CPC XXXXX, from GF1, level 49, x 5.8; **J.** CPC XXXXX, from GF1, level 59.7, x 2.3; **K.** CPC XXXXX, from GF1, level 59.7, x 3.0; **L.** CPC XXXXX, from GF1, level 59.7, x 4.9; **M.** CPC XXXXX, from GF1, level 59.7, x 3.4; **N.** CPC XXXXX, from GF1, level 59.7, x 3.8; **O.** CPC XXXXX, from GF1, level 46.9, hypostome showing maculae, x 8.9; **P.** CPC XXXXX, from GF1, level 46.9, hypostome, lateral view, x 8.9

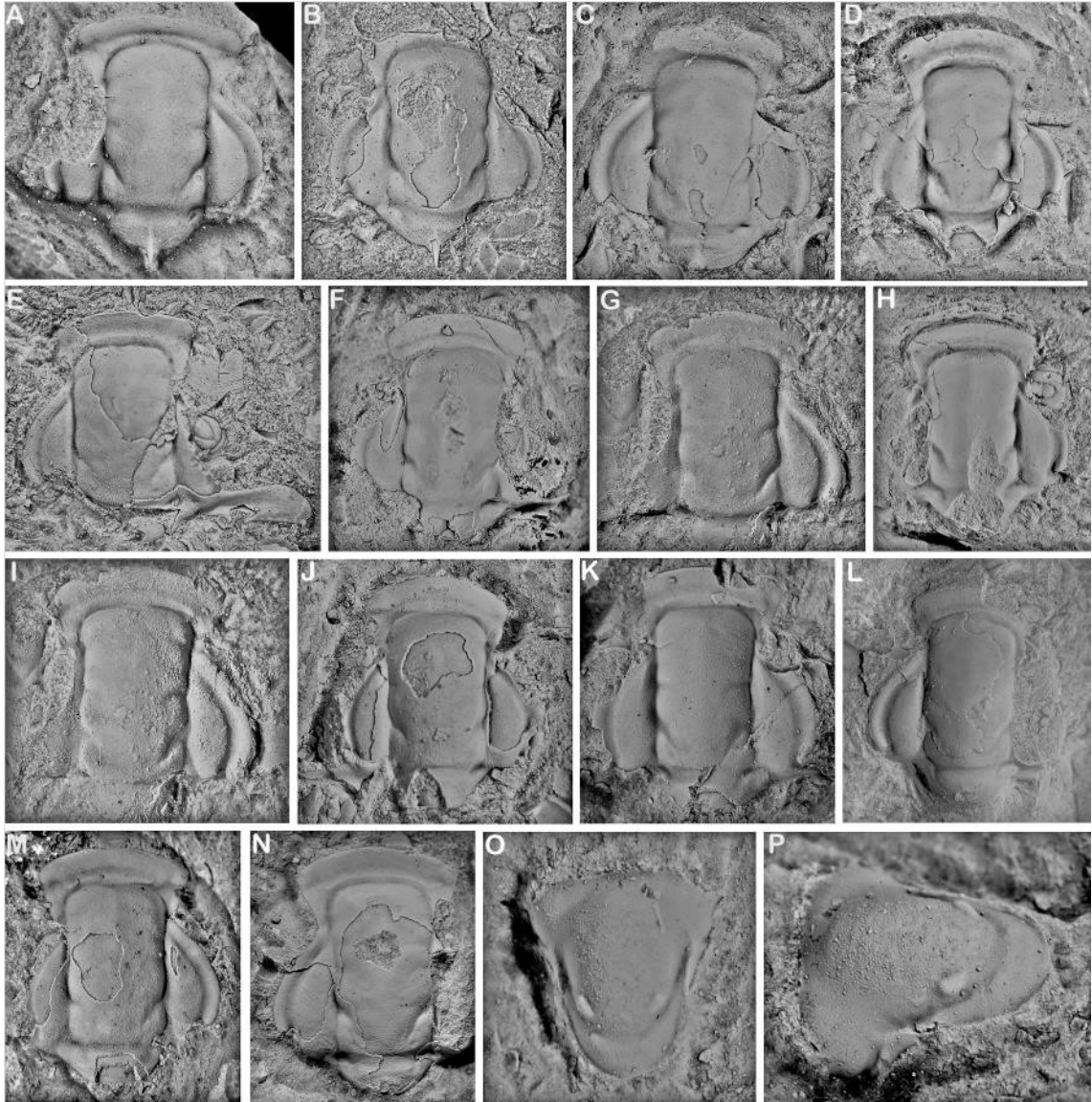


Figure 3-23. *Amphoton eminens*

Figure 3-24. *Amphoton eminens*: A. CPC XXXXX, from GF1, 59.7, pygidium, x 4.5; B. CPC XXXXX, from GF1, level 59.7, pygidium, x 5.1; C. CPC XXXXX, from GF1, level 59.7, pygidium, x 4.8; D. CPC XXXXX, from GF2, level 13.7, pygidium, x 4.3; E. CPC XXXXX, from GF1, level 59.7, left librigena, x 5.2; F. right librigena, x 4.9; G. CPC XXXXX, from GF1, level 59.7, close-up of librigenal border showing lack of ornament, x 18.0; H. CPC XXXXX, from GF1, level 59.7 (John Laurie Collection), close-up of anterior border showing lack of ornament, x 13.3.

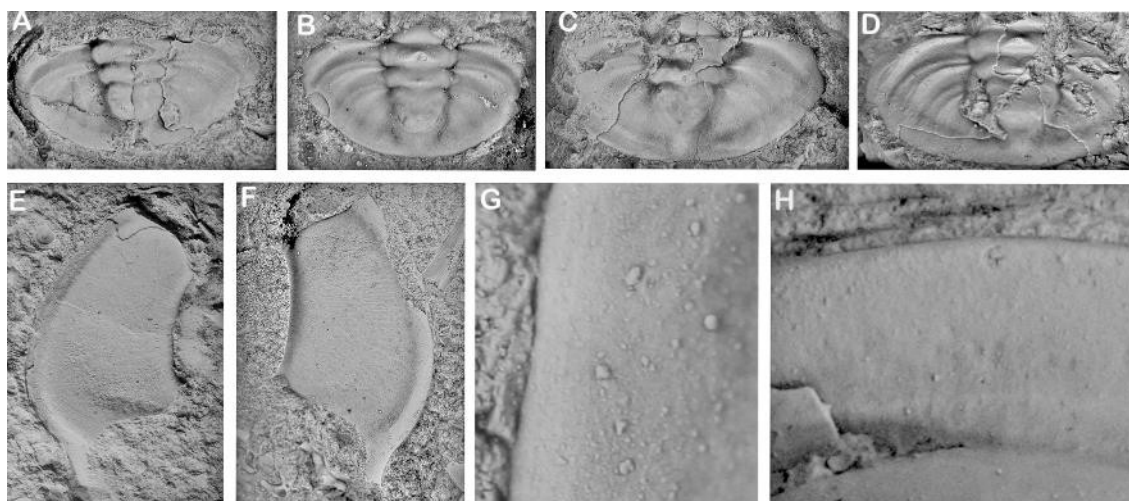


Figure 3-24. *Amphoton eminens*

Family DOLICHOMETOPIDAE Walcott, 1916

Fuchouia Resser & Endo in Kobayashi, 1935

2004 *Fuchouia*; Peng *et al.*, p. 60 (cum. syn.).

2004 *Fuchouia*; Jago *et al.*, p. 37.

2007 *Fuchouia*; Jago & Cooper, p. 479.

Type species. *Bathyriscus manchuriensis* Walcott, 1911.

Diagnosis. See Zhang & Jell (1987, p. 67) and comments in Jago *et al.* (2004) and Jago & Cooper (2007).

Remarks. Zhang & Jell (1987) and Peng *et al.* (2004) clarified the concept of *Fuchouia* and discussed fully the differences between *Fuchouia* and *Amphoton*. Their concept is followed herein. Peng *et al.* (2004b) listed and reviewed the species of *Fuchouia*. *Fuchouia* is known from China, Korea, Kazakhstan and Antarctica.

3.4.13. *Fuchouia fecunda* Öpik, 1982 (Fig. 3-25A-T, Fig. 3-26A-U)

1982 *Fuchouia fecunda*; Öpik, p. 27, pl. 6-8, pl. 9, fig. 1, pl. 10, figs 3-4, pls 11-13.

1982 *Fuchouia atopa* Öpik, p. 40, pl. 3, figs 7-9, pl. 9, fig. 3a-c, pl. 10, figs 1-2b.

2006 *Fuchouia fecunda* Öpik, Laurie, p. 177, fig. 46.

Material: 20 cranidia, 11 pygidia, 5 librigenae and one thorax with pygidium from GF1: 20.5– 64.9; GF2: 5.3 – 13.7; *T. gibbus* to *A. lower atavus* Zones.

Diagnosis. *Fuchouia* with anteriorly expanding glabella extending to anterior border furrow; palpebral lobes ca. 60% length of glabella. Lateral glabellar furrows almost effaced. Small occipital node. Semi-elliptical pygidium; four axial rings plus terminus. Four pair of well developed pleural furrows; three pairs of very shallow interpleural furrows.

Description. Largest cranidium 6.6mm long (sag.), subquadrate, moderately convex, width: length ca. 92–100% (n = 10), maximum width across posterior limbs of librigenae, narrowest forward of F2; anterior margin curved to almost straight, posterior margin of occipital ring curves strongly posteriorly. Anterior branches of facial sutures diverge at 20° before intersecting cranial margin; ϵ - ω diverge at ca. 180°. Glabella subquadrate, parallel sided and convex, with maximum convexity across midwidth lateral slopes gently curved; width:

length is 57–65% (av. = 60%, n = 9), occupying ca. 71% (n = 11) of cranial length; usually slightly expanded anterior of S3, with maximum width across anterolateral corners, broadly rounded anterior. Axial furrows narrow and moderately deep. S1 weakly defined or effaced, short, directed posteromedially, S3 sometimes effaced; Occipital ring of moderate width, narrowing abaxially, surmounted by a small short occipital spine; SO straight, shallow medially, wide (sag and exsag.). Preglabellar field narrow and sloping steeply to a border furrow of variable width which is parallel to the anterior margin. Anterior border narrow (sag. and exsag.) and convex, occupying 9–13% (n = 10) of cranial length (sag.). Palpebral lobe convex, 52–61% (n = 10) of cranial length (sag.), defined by moderately impressed palpebral furrow that intercepts axial furrow at or slightly posteriorly of S0. Entire cranium is punctate except for the furrows and the anterior border has a reticulating pattern.

Librigena up to 8mm long (exsag.), excluding genal spine; librigenal field slightly convex, trapeziform, occupying 81% of librigenal width. Pattern of caecae on field only. Lateral border wide and ornamented with the same reticulating pattern as the anterior border of the cranium, border furrow narrow and shallow. Thorax of nine segments.

Hypostome is 4.4 mm long (n = 1). Anterior border deflected ventrally.

Pygidium semielliptical, length (sag.): width (tr.) = 45–54% (av. = 49, n = 8). Anterolateral corners well defined, lateral margins gently curved to an evenly rounded posterior margin. Axis strongly convex (tr.), tapering rearward, occupying ca. 83 % of length (sag.) and ca. 26 % width (tr.) of pygidium. Articulating halfring short (sag.). Five axial rings plus terminus in adults, three or four in meraspid. Axial rings separated by shallow, narrow inter-ring furrows. Terminal piece short. Four pairs of well developed pleural furrows in adults; three pairs of shallow interpleural furrows. Indistinct pygidial furrow.

Remarks. The Gowers specimens are confidently assigned to *Fuchouia fecunda*, which Öpik (1982) described in detail. *Fuchouia fecunda* is part of a group of Chinese, Australian and Antarctic species of *Fuchouia* that have relatively long palpebral lobes, short (exsag.) posterior areas of the fixigenae and pygidia without a border. This group includes *Fuchouia limbatus* Lu *et al.* 1974, *F. elongata* Lu & Qian (in Lu *et al.*, 1974),

F. labda Öpik, 1982, *F. morstonensis* Öpik, 1982, *F. tasmaniensis* Jago & Bao (in Jago *et al.* 2004) and *F. lantermanensis* Jago (in Jago & Cooper, 2007). The presence of long palpebral lobes *Fuchouia fecunda* has previously caused confusion with species of *Amphoton*. The generic concept of *Fuchouia* and *Amphoton* has been discussed by Öpik (1982), Zhang and Jell (1987) and Peng *et al.* (2004), and it is followed here. The Gowers specimens show an additional feature not previously mentioned by other authors - the ornament on the anterior cranial border and the librigenal border (see Fig. 3-26 T, U) are characteristic of *F. fecunda*.

Figure 3-25. *Fuchouia fecunda*: crania: **A.** CPC XXXXX, from GF2, level 13.7, showing left lateral projection, x 5.5; **B.** CPC XXXXX, from GF1, level 53.3, x 5.9; **C.** CPC XXXXX, from GF2, level 13.7, showing partial left lateral projection, x 7.7; CPC XXXXX, from GF2, level 13.7, x 5.3; **E.** CPC XXXXX, from GF1, level 53.3, damaged cranidium, showing left lateral projection, x 4.9; **F.** CPC XXXXX, from GF1, level 64.9, x 2.8; **G.** CPC XXXXX, from GF1, level 64.9, x 5.0; **H.** CPC XXXXX, from GF1, level 64.9, x 4.4; **I.** CPC XXXXX, from GF1, level 64.9, right lateral projection, x 7.1; **J.** CPC XXXXX, from GF2, level 13.7, x 6.4; **K.** CPC XXXXX, from GF2, level 13.7, x 4.2; **L.** CPC XXXXX, from GF1, level 59.7, x 10.4; **M.** CPC XXXXX, from GF1, level 59.7, x 3.9; **N.** CPC XXXXX, from GF2, level 13.7, x 4.6; **O.** CPC XXXXX, from GF1, level 64.9, x 5.4; **P.** CPC XXXXX, from GF2, level 13.7, x 6.0; **Q.** CPC XXXXX, from GF2, level 13.7, showing right lateral projection, x 7.9; **R.** CPC XXXXX, from GF1, level 53.3, x 4.9; **S.** CPC XXXXX, from GF1, level 64.9, x 5.2; **T.** CPC XXXXX, from GF1, level 59.7, x 4.2.

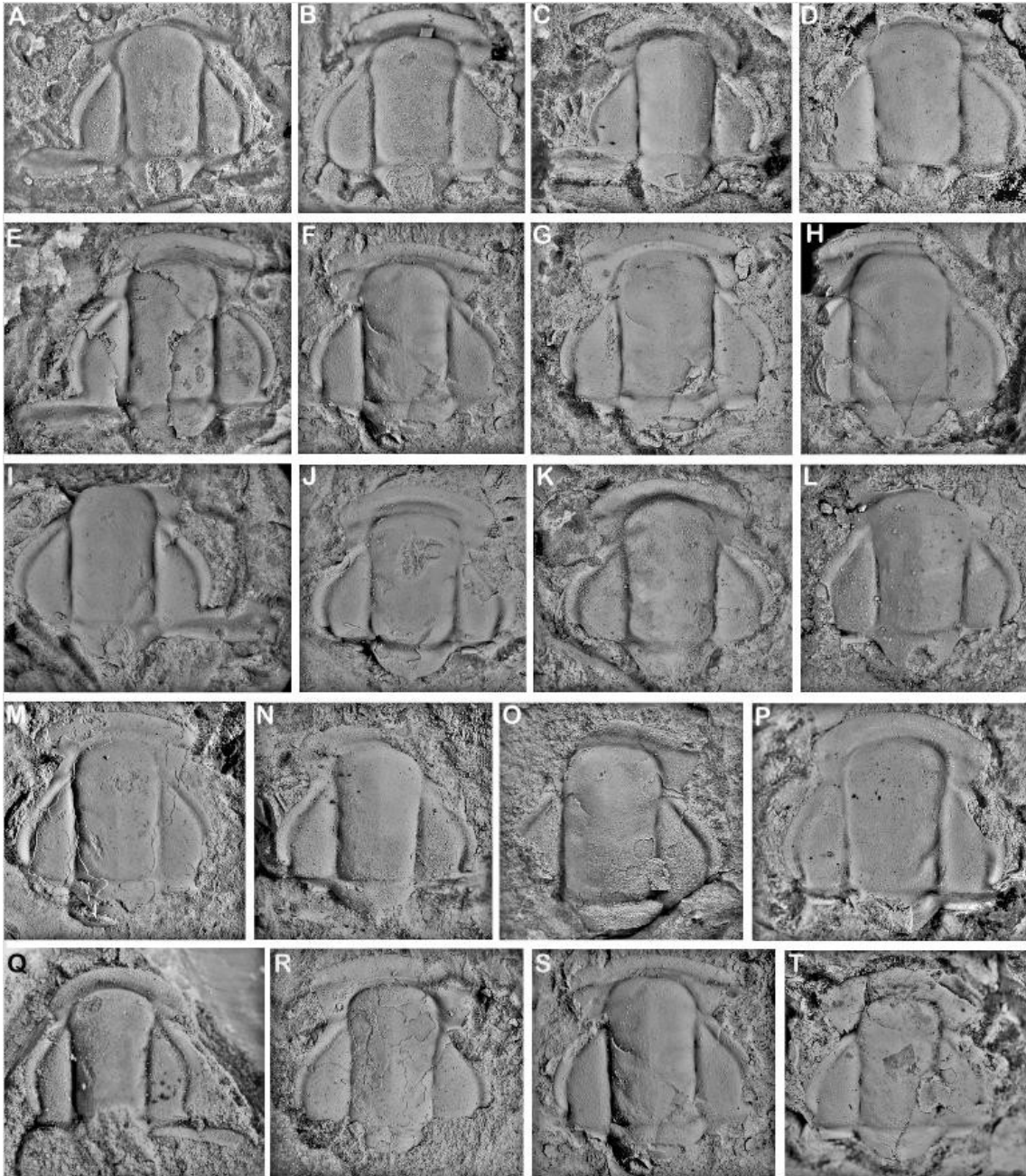


Figure 3-25. *Fuchouia fecunda*

Figure 3-26. *Fuchouia fecunda*: **A.** latex cast of of CPC XXXXX, from GF1, level 20.5, pygidium and partial thorax, x 7.7; **B.** CPC XXXXX, from GF1, level 64.9, pygidium, x 10.0; **C.** CPC XXXXX, from GF1, level 59.7, pygidium, x 9.4; **D.** CPC XXXXX, from GF2, level 13.7, pygidium, x 4.8; **E.** CPC XXXXX, from GF2, level 13.7, pygidium, x 13.1; **F.** CPC XXXXX, from GF1, level 22.5, thorax and pygidium, x 5.1; **G.** CPC XXXXX, from GF2, level 13.7, pygidium, x 6.3; **H.** CPC XXXXX, from GF2, level 13.7, pygidium, x 8.1; **I.** CPC XXXXX, from level GF1, level 56.3, pygidium, x 4.2; **J.** CPC XXXXX, from GF2, level 13.7, pygidium, x 12.5; **K.** CPC XXXXX, from GF1, level 56.3, pygidium, x 11; **L.** CPC XXXXX, from GF2, level 13.7, pygidium, x 7.5 ; **M.** CPC XXXXX, from GF2, level 13.7, pygidium, x 9.4; **N.** CPC XXXXX, from GF2, level 13.7, left librigena, x 10.8; **O.** CPC XXXXX, from GF2, level 13.7, left librigena, x 9.1; **P.** CPC XXXXX, from GF1, level 59.7, left librigena, x 16.0; **Q.** CPC XXXXX, from GF2, level 13.7, right librigena, x 12.8; **R.** CPC XXXXX, from GF1, level 64.9, right librigena, x 5.1; **S.** CPC XXXXX, from GF1, level 64.9, hypostoma, x 7.4; **T.** close-up of frontal border on specimen CPC XXXXX, from GF1, level 59.7, showing ornament, x 26; **U.** librigenal border of specimen CPC XXXXX, from GF1, 59.7, showing ornamentation, x 24.

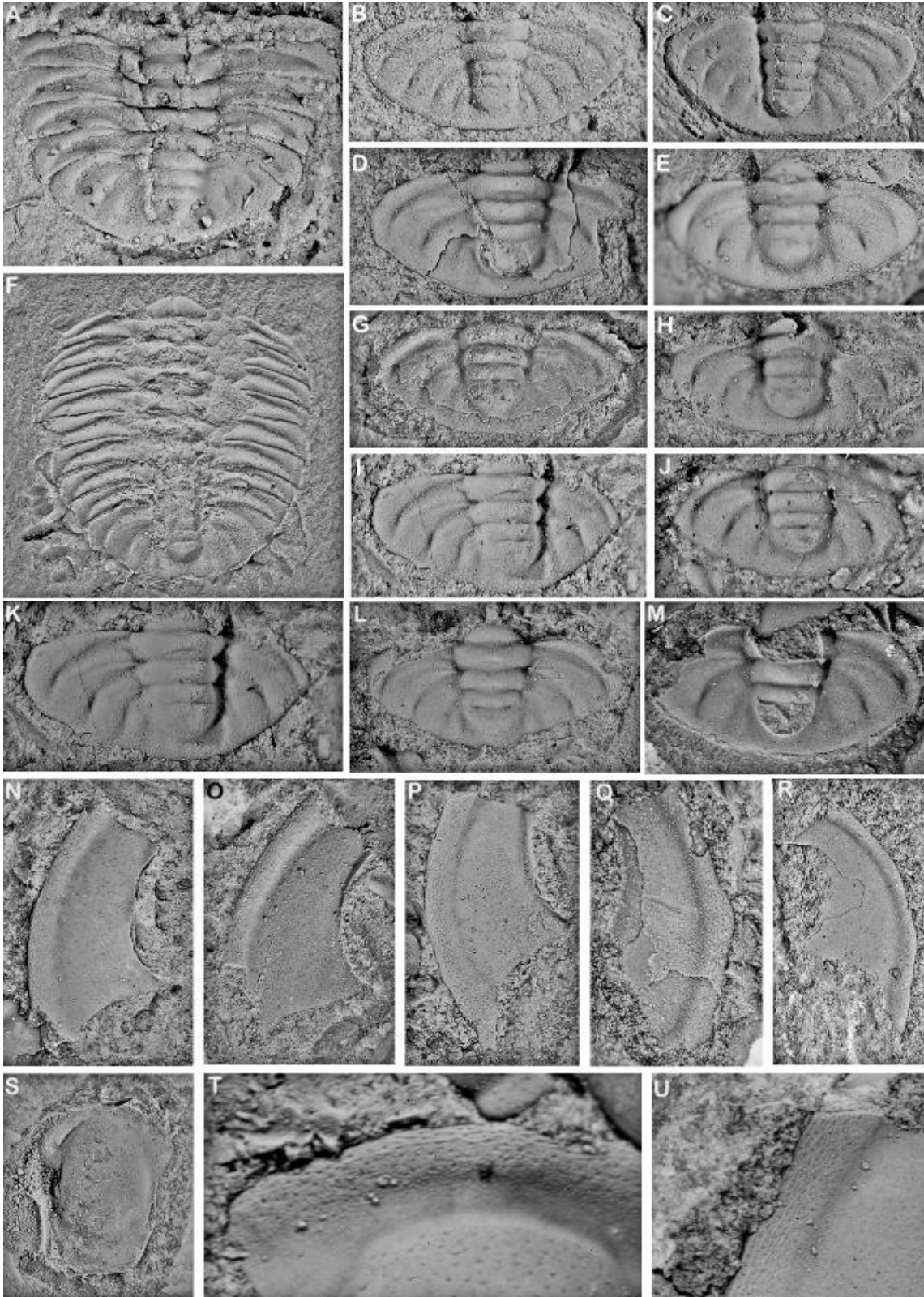


Figure 3-26. *Fuchouia fecunda*

Family DORYPYGIDAE Kobayshi, 1935

3.4.14. *Dorypyge* Dames, 1883 (Fig. 3-27)

Type species. *Dorypyge richthofeni* Dames, 1883, Middle Cambrian, Changhia Formation, Liaoning, China.

Material. CPCXXD1, One pygidium from GF2: 17.6; lower *A. atavus* zone.

Remarks. This pygidium is tentatively assigned to *Dorypyge* due to its similarity to *Dorypyge pergranosa* Resser & Endo, 1937 (see Zhang & Jell 1987, pl. 15-figs 2, 3, 5, 8) particularly the ornament, possession of three pygidial rings, and the marginal spines.



Figure 3-27. *Dorypyge* sp. A. pygidium CPCXXXXX, from GF2, level 13.7, showing pustulate ornament, x 9.1.

Superfamily ANOMOCAROIDEA Poulsen, 1927

Family ANOMOCARIDAE Poulsen, 1927

Chondranomocare Poletaeva, 1956

Type species. *Chondranomocare bidjensis* Poletaeva (in Chernysheva *et al.*, 1956).

3.4.15. *Chondranomocare confertum* (Whitehouse, 1939) (Fig.3-28A-D)

1939 *Anomocare confertum* Whitehouse, p. 223, pl. 23, figs. 22-28.

1978 *Chondranomocare confertum* (Whitehouse); Jell and Robison, p. 12, pl. 3, figs 1-19.

2006 *Chondranomocare confertum* (Whitehouse); Laurie, p. 178, fig. 49. *Material*. CPCXXCC1-4. Four cranidia from GF1: 59.7; lower *A. atavus* Zone. *Diagnosis*. See Jell and Robison (1978, p. 11).

Remarks. Jell and Robison (1978) presented a comprehensive description of this species. The Gowers specimens fit well within the morphological variation shown by their illustrated specimens. Laurie's (2006) specimens from a level high in the Arthur Creek section, most likely upper *T. gibbus* or *A. atavus* in age, are conspecific.

Figure 3-28. *Chondranomocare confertum*: Four cephalae, **A.** CPCXXXXX x 4.5; **B.** CPCXXXXX, showing well developed furrows, x 4.8; **C.** CPCXXXXX, from GF1, 59.7, x 2.5; **D.** latex cast of CPCXXXXX x 3.2. A, B and D from John Laurie Collection, GF1, level 59.7

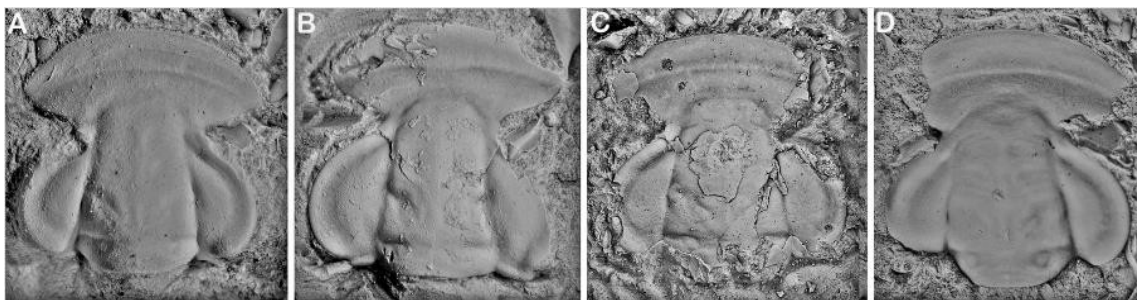


Figure 3-28. *Chondranomocare confertum*

Order PTYCHOPARIIDA Swinnerton, 1915

Suborder PTYCHOPARIINA Richter, 1932

Family PTYCHOPARIIDAE Matthew, 1887

Asthenopsis Whitehouse, 1939

2014 *Asthenopsis* Whitehouse; Bentley & Jago, p. 284 (cum. syn.)

Type species. *Asthenopsis levior* Whitehouse, 1939, p. 214, pl. 22, fig. 17–20.

Diagnosis. See Bentley & Jago, 2014, p. 284.

3.4.16. *Asthenopsis southgatei* sp.nov. (Fig 3-29A-T, Fig.3-30A-M)

Derivation of name. In honour of Peter Southgate for his work on the Cambrian stratigraphy of the Georgina Basin, especially the Gowers Formation.

Holotype. CPCXXXXX, Fig. 29A.

Paratype. CPC XXXXX, Fig. 29C.

Material. CPCXXAS1-33, four entire specimens, 20 cephalae, 7 pygidia, two librigenae from GF1: 11.2—49, GF2: 1.2—17.6; *T. gibbus* to lower *A. atavus* Zone.

Diagnosis. *Asthenopsis* with rounded anterolateral glabellar corners, long (sag.) anterior border, moderate convexity, anterior branches of facial suture diverging forward and abaxially convex, relatively short palpebral lobes, ornament of very closely spaced papillae over entire surface except apodemal areas and furrows, and coarse perforated tubercles interspersed sparsely over the same areas. Pleural tips rounded. Transverse pygidium with convex pleural areas.

Description. Entire length of largest specimen = 26mm (Fig. 30M). Largest cranidium ~ 5mm long (sag.). Cranidium with moderately steep anterior slope in lateral profile. Width: length

= 128% (n = 4). Anterior margin gently curved, posterior margin of occipital lobe usually strongly curved backwards but variable. Anterior branches of facial sutures diverge at ca. 90° before intersecting cranial margin; $\epsilon - \omega$ diverge from one another at ca. 180° . Glabella trapeziform, with maximum width at SO, tapering evenly to the anterior glabellar margin to about 60% of its basal width; width: length of 100% (n = 8), occupying about 51% of cranial length; anterior glabella straight to slightly rounded, anterolateral corners of the glabella are quite broadly rounded. Axial furrows narrow and usually moderately deep but can be shallow. S1 well defined, directed posteromedially to about one-third of the distance to glabellar width where they bifurcate, with one branch continuing for the same distance strongly posteromedially and the other directed a shorter distance less posteromedially. S2 and S3 less strongly defined, parallel to the shorter branch of S1. Glabellar furrows smooth. Occipital ring of moderate width (sag.), narrowing abaxially, with a small central occipital node; SO straight. Occipital furrow wide (sag.), shallow in midwidth, very deep laterally, forming what appears to be a pair of apodemal pits.

Preglabellar and preocular field slope down to a shallow, narrow border furrow that runs parallel to the anterior margin, with a pattern of anastomosing caecae. Anterior border wide (sag. and exsag.) and flat, occupying 13–18% (av. = 14, n = 18) of the cranial length (sag.). Palpebral lobe strongly curved, about 29% of total cranial length (exsag.), wide (tr.). Palpebral area of fixigena convex, sloping posterolaterally. Eye ridges prominent, low and wide, anterior edges meeting glabella at fossulae. Posterolateral projection of fixigena downsloping, expanding abaxially. Posterior border narrow (exsag.), separated from fixigenal field by wide border furrow which widens abaxially. Librigena slightly convex, width about equal to maximum glabellar width with wide, flattened and ornamented border. Caeca

cover librigena, except for border. Ornament of papillae and sparse perforated tubercles over cranidium except on furrows, palpebral lobe and distal parts of posterior limb.

Thorax of 14 segments. Pleurae project laterally with a small decrease in size posteriorly. Axial ring of each thoracic segment well defined and of approximately constant length (sag. and exsag.); rings becoming progressively narrower (tr.) posteriorly, such that axial ring of the posteriormost segment is ca. 60% width of T1 axial ring. Axial furrows deep and well defined. Pleural furrows wide.

Pygidium transverse, subovate in outline, slightly convex, length (sag.): width (tr.) = 33–39% (av. = 36, n = 5). Axis short, broad, strongly convex, tapered, occupying 75 % of pygidial length (sag.). Pleural areas flattened with the first interpleural furrow wide and well defined, almost reaching pygidial margin, and second interpleural furrow poorly impressed and shorter. Articulating half-ring well defined, separated from first axial ring by deep, broad furrow. First axial ring separated by a deep, narrow inter-ring furrow from second axial ring but next inter-ring furrow less defined. Axial furrow shallow and not well defined around rear of terminal piece. Pygidial margin gently rounded with a tendency to become straight in the mid- posterior section. The anterior border of pleural area bends at a large obtuse angle midwidth (tr.). Ornament of fine and coarse papillae covering pygidium with the coarse papillae denser at margin.

Remarks. Cranidia from the Gowers Formation are most similar to those of *Asthenopsis rhinostrongyla* (Jell, 1978, pl. 34, figs 2-7, pl. 35, fig.1, 2) in general shape, number and orientation of the glabellar furrows, size and shape of the palpebral lobes, and ornament of punctae. *A. southgatei* differs in having divergent anterior facial sutures, a more tapered glabella, the central position of the occipital node, the lack of paired eye ridges, pygidial width and shape, and most noticeably in the longer length (sag.) of the anterior border. Fig. 3-

31 shows the anterior border lengths (as a percentage of cranial length) of all species illustrated by Jell (1978) and those of the new species. It is clear that *A. southgatei* differs substantially in this character.

Laurie (2006, p. 189, fig. 57) illustrated a similar species as Ptychoparioid sp. 2 which possibly belongs to *A. southgatei* due to its similarly long cephalic border, transverse pygidium and ornament, but the glabella appears to be less tapered.

Figure 3-29. *Asthenopsis southgatei* n. sp.: Cranidia: **A.** Holotype specimen CPC XXXXX, from GF2, level 13.7, showing well developed glabellar furrows and eye ridges, x 4.2. **B.** Paratype specimen CPC XXXXX, from GF2, level 13.7, x 3.2. **C.** CPC XXXXX, from GF2, level 13.7, showing a well-developed occipital node and ornament, x 2.4. **D.** CPC XXXXX, from GF2, level 13.7, showing partial right lateral projection and ornament, x 6.0. **E.** CPC XXXXX, from GF2, level 15.8, showing well- developed occipital node and ornament, x 1.3. **F.** CPC XXXXX, from GF2, level 13.7, damaged glabella, x 4.0. **G.** CPC XXXXX, from GF2, level 13.7, showing left lateral projection and ornament, x 3.0. **H.** CPC XXXXX, from GF2, level 13.7, showing broken right lateral projection x 2.6. **I.** CPC XXXXX, from GF2, level 13.7, x 2.9. **J.** CPC XXXXX, from GF2, level 13.7, showing well developed glabellar furrows, x 5.4. **K.** CPC XXXXX, from GF2, level 13.7, showing well developed glabellar furrows, x 3.8. **L.** CPC XXXXX, from GF2, level 13.7, x 2.9. **M.** CPC XXXXX, from GF2, level 13.7, x 3.4. **N.** CPC XXXXX, from GF2, level 13.7, x 5.2. **O.** CPC XXXXX, from GF2, level 13.7, x 3.7. **P.** CPC XXXXX, from GF2, level 13.7, x 8.2. **Q.** CPC XXXXX, from GF2, level 10.8, showing ornament, x 3.3. **R.** CPC XXXXX, from GF2, level 13.7, x 3.0. **S.** CPC XXXXX, from GF2, level 13.7, x 7.1. **T.** CPC XXXXX, from GF2, level 12.2, x 4.2.

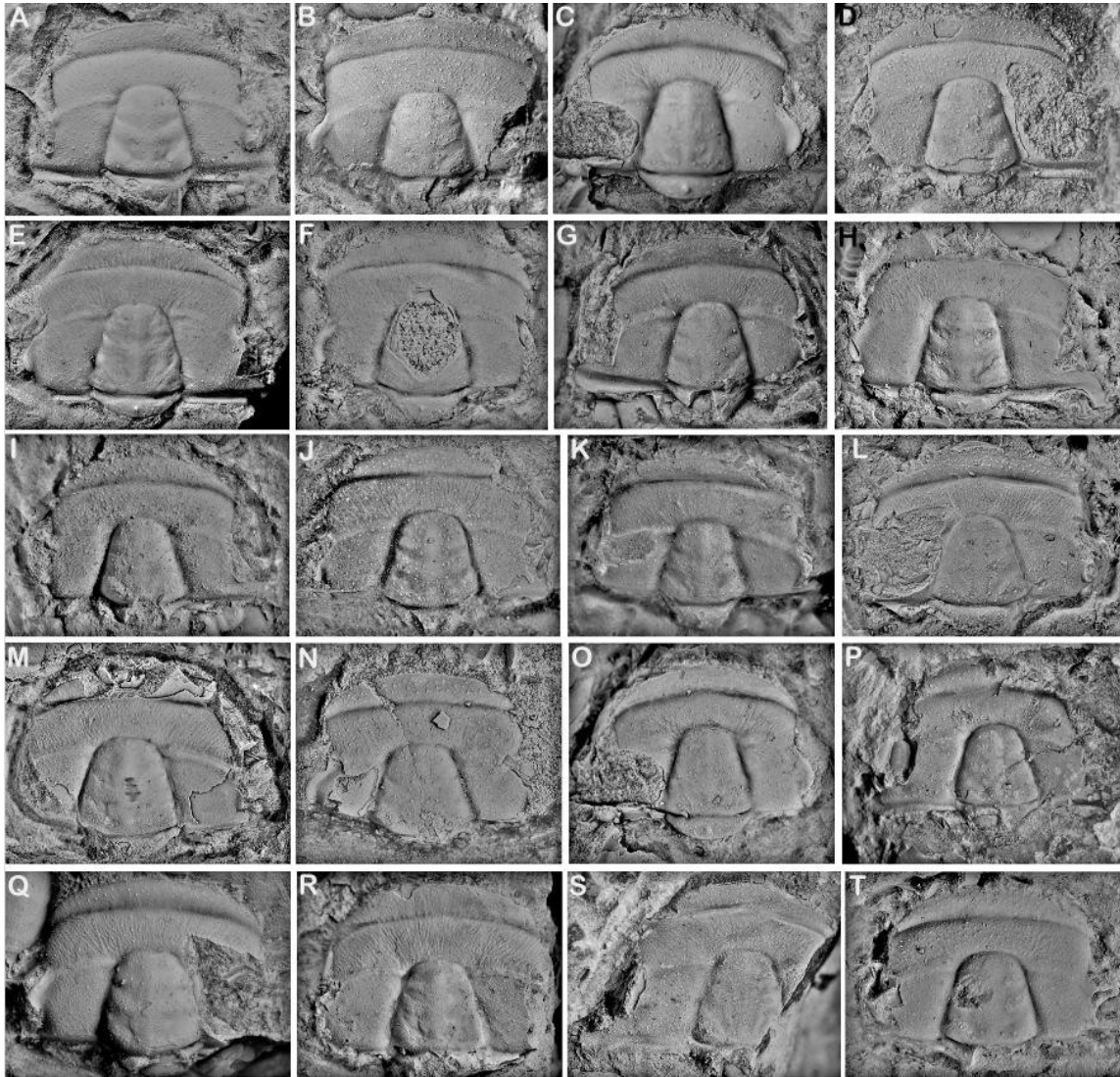


Figure 3-29. *Asthenopsis southgatei* n. sp.

Figure 3-30. *Asthenopsis southgatei* n. sp.: **A.** CPC XXXXX, from GF2, level 13.7, pygidium, x 8.6. **B.** CPC XXXXX, from GF2, level 17.6, x 8.7. **C.** CPC XXXXX, from GF2, level 13.7, left librigena, x 6.4. **D.** CPC XXXXX, from GF2, level 13.7, left librigena, x 4.0. **E.** CPC XXXXX, from GF2, level 13.7, pygidium, x 5.6. **F.** CPC XXXXX, from GF2, level 13.7, latex cast of pygidium, x 7.1. **G.** CPC XXXXX, from GF2, level 13.7, x 4.8. **H.** CPC XXXXX, from GF2, level 13.7, pygidium, x 6.5. **I.** CPC XXXXX, from GF2, level 13.7, damaged pygidium, x 7.1. **J.** CPC XXXXX, from GF1, level 11.2, damaged complete exoskeleton, x 2.2. **K.** CPC XXXXX, from GF1, level 20.5, broken complete exoskeleton, x 3.4. **L.** CPC XXXXX, from GF1, level 11.2, complete exoskeleton, x 4.4. **M.** CPC XXXXX, from GF1, level 11.2, cranium, thorax and pygidium, x 2.1.

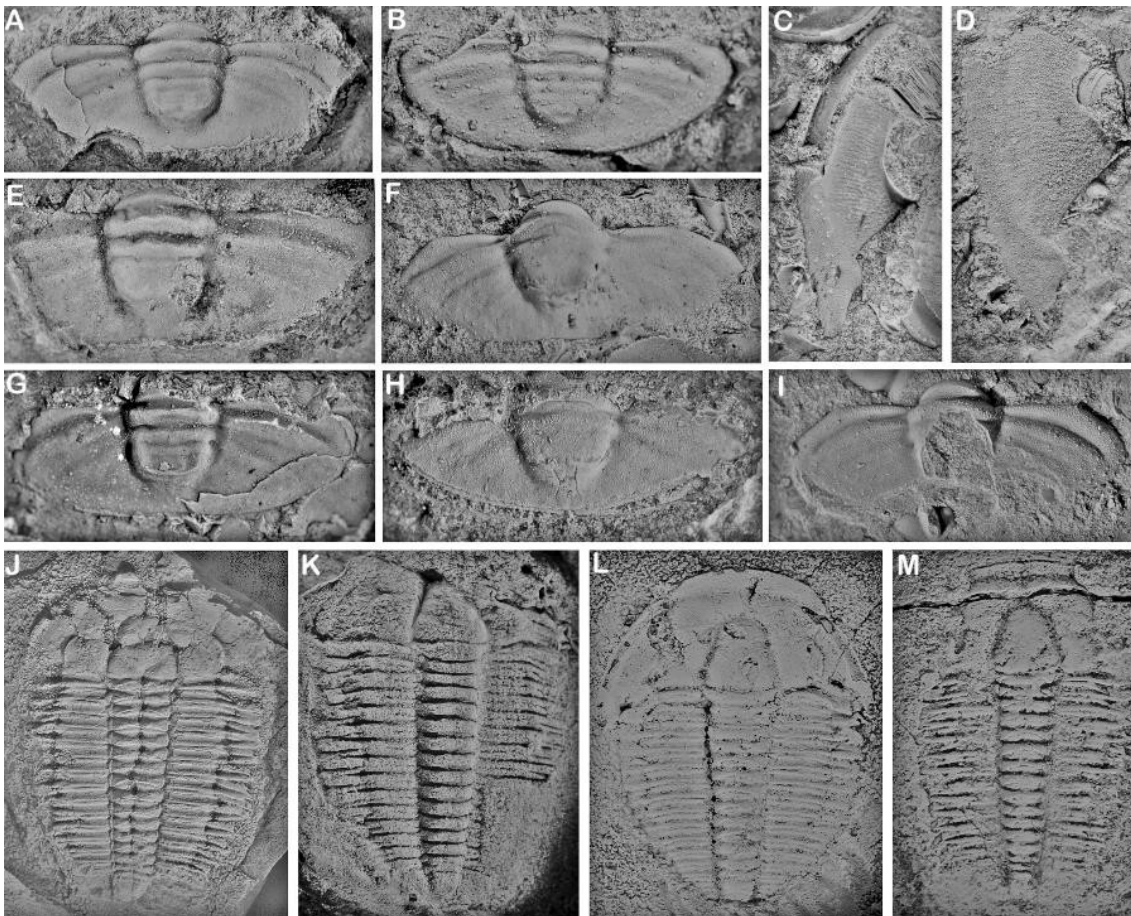


Figure 3-30. *Asthenopsis southgatei* n. sp.

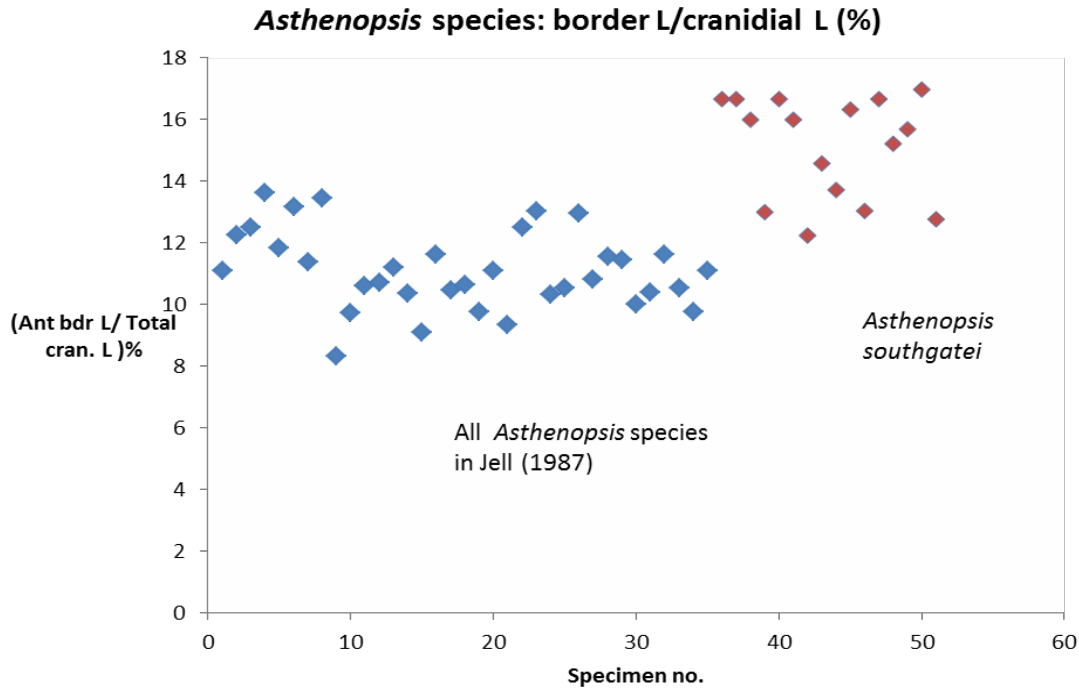


Figure 3-31. Graph of the anterior border length as a percentage of cranial length, for all *Asthenopsis* species described by Jell (1978) and for specimens of *Asthenopsis southgatei* n. sp. from the Gowers Formation

Order PTYCHOPARIIDA Swinnerton, 1915

Suborder PTYCHOPARIINA Richter, 1932

Superfamily PTYCHOPARIOIDEA Matthew, 1887

Family NEPEIDAE Whitehouse, 1939

Penarosa Öpik, 1970

Synonymy. See Paterson (2005, p. 498).

Type species. *Penarosa retifera* Öpik, 1970, p. 25.

Diagnosis. See Paterson (2005, p. 498).

3.4.17. *Penarosa retifera* Öpik, 1970 (Fig. 3-32A-O)

Material. CPCPR1 – 15, 14 cephalia, one librigena; GF1: 59.7, GF2-: 3.7; lower *A. atavus* Zone.

Remarks. Paterson (2005) recently provided a full description of *Penarosa retifera*, including material from the Gowers Formation (GF1), thus no further discussion is required here.

Figure 3-32. *Penarosa retifera*: A – G, I, K, N, O, are cranidia from GF1, level 59.7 (collected by Dr. J. Paterson): **A.** CPC 37124, x 2.7; **B.** CPC 37123, x 2.3; **C.** CPC 37121, x 2.6; **D.** CPC 37124, x 2.5; **E.** CPC 37136, x 3.3; **F.** CPC 37134, x 2.5; **G.** CPC 37133, x 7.2; **H.** CPC XXXXX, from GF1, level 59.7 x 1.5; **I.** CPC 37126, x 6.8; **J.** CPC XXXXX, from GF1, level 59.7, x 13.0; **K.** CPC 37125, x 3.2 **L** right librigena, CPCXXXXX, found with specimens CPC 37119 – 121, x 3.6; **M** CPC XXXXX, from GF1, level 59.7, x 13.3; **N.** CPC 37128, x 5.6; **O.** CPC 37116, x 6.8.

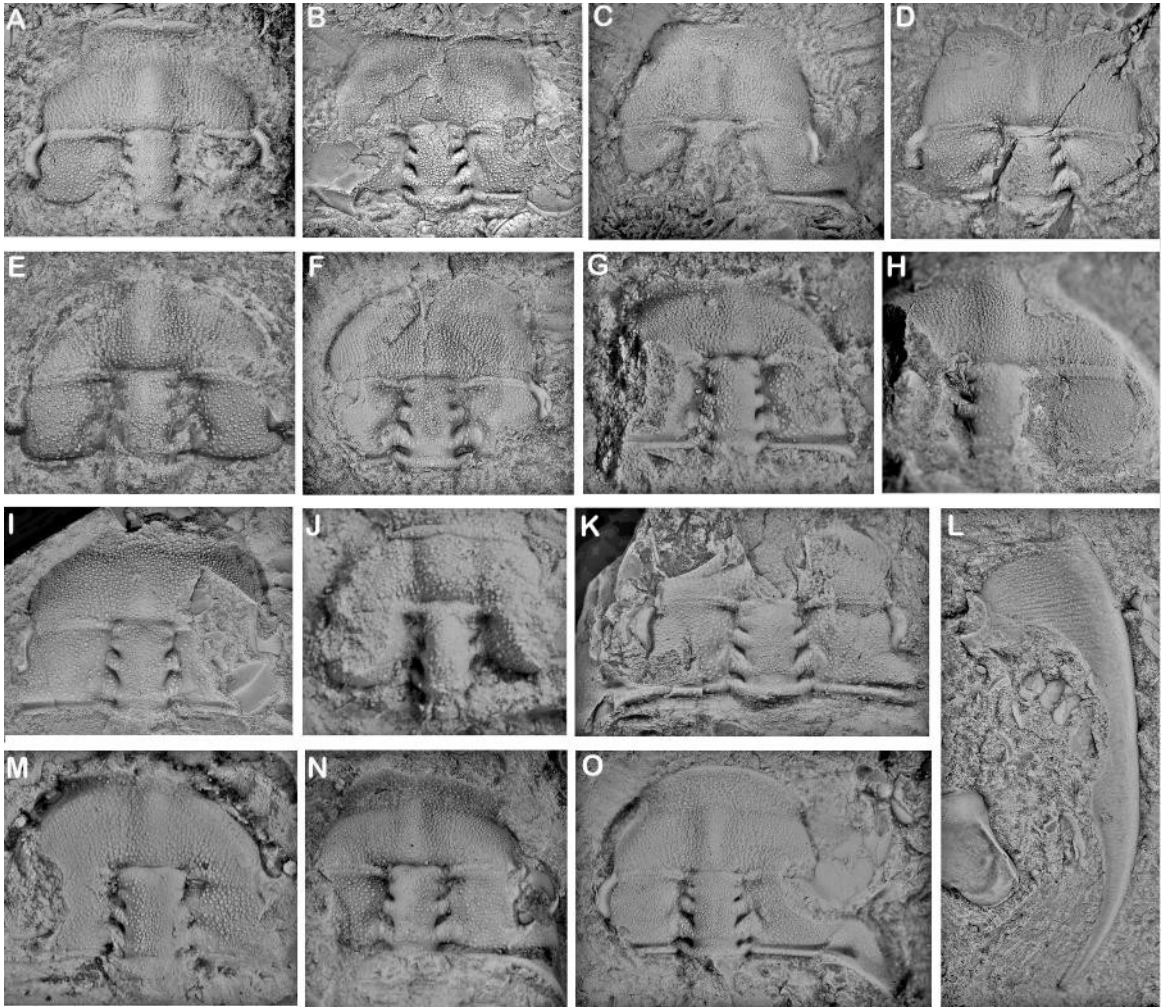


Figure 3-32. *Penarosa retifera*

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Chapter 4. Biodiversity, biofacies and biogeography of middle Cambrian (Series 3) arthropods (Trilobita and Agnostida) on the East Gondwana margin



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