Trilobites of the Holm Dal Formation (late Middle Cambrian), central North Greenland

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An unusually diverse trilobite fauna in the Holm Dal Formation is dominated by polymeroid genera and species that are most characteristic of the lower and middle *Cedaria* Zone as widely applied in North America. Several agnostoid species are characteristic of the upper *Lejopyge laevigata* Interval-zone of Robison (1984), and correlation with the Swedish standard for north-western Europe indicates a late Middle Cambrian age.

Biogeographic analysis shows that continental endemism of the 34 polymeroid genera and 43 polymeroid species in the Holm Dal Formation exceeds 88 and 97 percent respectively. In marked contrast, all 12 of the Holm Dal agnostoid genera and at least 13 of the 15 agnostoid species have intercontinental distributions (0 and 13 percent endemism respectively). Comparisons with coeval North American faunas suggest that Middle Cambrian biozones based on polymeroid species may be useful on a regional scale, but probably will not be applicable on a continental scale. Genus-based polymeroid zones may be applicable on a continental scale, but long stratigraphic ranges of genera will limit precision. Species-based agnostoid zones will be applicable globally, but probably will be most useful in deposits representing the neritic to oceanic transition.

Fifty-eight trilobite species, some in open nomenclature, are described from Peary Land and Freuchen Land. Of the taxa represented, 9 of 34 genera are new: *Balderia, Conopolus, Durinia, Holmdalia, Pearylandia, Tavsenia, Toragnostus, Verditerrina,* and *Wandelella*. Twenty-four species are new: *Balderia aspera, Blountia bella, Bolaspidella stymacantha, Cedaria major, Cedaria tumicephala, Conopolus granulus, Crepicephalus eos, Durinia granulosa, Elrathia omega, Glaphyraspis alpha, Madarocephalus scolus, Marjumia brevifrons, Marjumia spinosa, Matania matuta, Matania quadrata, Modocia planata, Nixonella furta, Olenoides ternus, Onchonotopsis physala, Pearylandia parva, Syspacheilus catatate, Tavsenia ditrema, Verditerrina lacinia,* and *Wandelella compta*. In addition, the new species *Conopolus rasettii* is described from Quebec, Canada. A lectotype is designated for *Proagnostus bulbus* Butts 1926, the type species of *Proagnostus*.

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The Holm Dal Formation of central North Greenland is defined in an accompanying paper by Ineson (this volume), who provides locality and stratigraphic information for the trilobites described here. Associated brachiopods are described by Zell & Rowell (this volume) and molluscs by Peel (this volume). Trilobite and lithofacies relationships in the Holm Dal have been evaluated by use of multivariate techniques (Hood & Robison, this volume).

One of the most diverse trilobite faunas known from the late Middle Cambrian is present in the Holm Dal Formation (Table 1). Preservation of specimens is moderately good to excellent. The agnostoid trilobites provide evidence of connection with open-shelf faunas of the world and include several species having important biostratigraphic significance. The numerous polymeroid trilobites have their closest affinities with faunas of North America and show some previously unreported associations of genera.

Depositional environments

Major lithofacies and biofacies patterns indicate that Greenland and North America were united in a single continent during Cambrian time (e.g. Palmer 1974). Palaeogeographic reconstructions for the period show this continent, Laurentia, in equatorial latitudes (e.g. Bambach et al. 1980). Lithofacies indicate that the Laurentian craton was encircled by a broad marine shelf. Shallow-water carbonate platforms commonly separated shoreward muddy lagoons from open-shelf and slope environments (e.g. Robison 1976). Evidence from

Table 1. Classification of trilobites in the Holm Dal Formation.

- Order Agnostida
  - Family Agnostidae
    - *Agnostus exsulatus* Poulsen
    - *Homagnostus* sp.
  - Family Diplagnostidae
    - *Diplagnostus planicauda* (Angelin)
    - *Oedorhachis typicalis* Resser
    - *Oidalagnostus trispinifer* Westergård
    - *Proagnostus bulbus* Butts
  - Family Peronopsidae
    - *Ammagnostus beltensis* (Lochman)
    - *Kormagnostus seclusus* (Walcott)
    - *Peronopsis incertus* (Robison)
    - *Peronopsis tenuis* (Illing)
  - Family Ptychagnostidae
    - *Lejopyge armata* (Linnarsson)
    - *Lejopyge dubia* (Whitehouse)
    - *Lejopyge laevigata* (Dalman)
    - *Tomagnostella exsculpta* (Angelin)
  - Family uncertain
    - *Toragnostus bituberculatus* (Angelin) n. gen.
- Order Polymerida
  - Family Asaphiscidae
    - *Blountia bella* n. sp.
    - *Blountia* sp. 1
    - *Blountia* sp. 2
  - Family Catillicephalidae
    - *Catillicephala rotunda* (Rasetti)
    - *Madarocephalus scolus* n. sp.
  - Family Cedariidae
    - *Bonneterrina* sp.
    - *Cedaria major* n. sp.
    - *Cedaria prolifica* Walcott
    - *Cedaria tumicephala* n. sp.
  - Family Crepicephalidae
    - *Crepicephalus eos* n. sp.
  - Family Dolichometopidae
    - *Athabaskiella obsoleta* (Raymond)
  - Family Dorypygidae
    - *Olenoides ternus* n. sp.
  - Family Kingstoniidae
    - *Ankoura* sp.
    - *Bynumia metisensis* Rasetti
    - *Kingstonia peltata* Palmer
  - Family Llanoaspidae
    - *Nixonella furta* n. sp.
  - Family Lonchocephalidae
    - *Agelagma quadratum* Öpik
    - *Glaphyraspis alpha* n. sp.
    - *Hawkinsia?* sp.
    - *Welleraspis newfoundlandensis* (Lochman)
  - Family Marjumiidae
    - *Marjumia brevifrons* n. sp.
    - *Marjumia spinosa* n. sp.
    - *Modocia planata* n. sp.
    - *Pearylandia parva* n. gen. n. sp.
    - *Syspacheilus catatate* n. sp.
  - Family Menomoniidae
    - *Bolaspidella stymacantha* n. sp.
    - *Tavsenia ditrema* n. gen. n. sp.
  - Family Onchonotopsididae
    - *Cryptoderaspis metisensis* Rasetti
    - *Durinia granulosa* n. gen. n. sp.
    - *Matania matuta* n. sp.
    - *Matania quadrata* n. sp.
    - *Onchonotopsis pergibba* Rasetti
    - *Onchonotopsis physala* n. sp.
  - ?Family Solenopleuridae
    - *Balderia aspera* n. gen. n. sp.
  - Family uncertain
    - *Conopolus granulus* n. gen. n. sp.
    - *Elrathia marjumi* Robison
    - *Elrathia omega* n. sp.
    - *Exigua quebecensis* (Rasetti)
    - *Hemirhodon* sp.
    - *Holmdalia punctata* (Rasetti) n. gen.
    - *Verditerrina lacinia* n. gen. n. sp.
    - *Wandelella compta* n. gen. n. sp.
    - Undetermined pygidium

lithology and faunas of the Holm Dal Formation further supports such interpretations.

According to Ineson (this volume), who provides supporting evidence, the Holm Dal Formation represents deposition in an open-marine, mainly low-energy environment beneath normal wave base. An outer shelf to slope setting is envisaged. The depositional gradient was low. Poor circulation commonly resulted in oxygen-deficient waters. Deposition was mainly from suspension currents and less commonly from dilute density currents or storm currents. Intercalated breccia deposits represent rare and localized mass-flow events.

Most trilobites from the Holm Dal Formation are preserved in either lime mudstone or lime grainstone. In mudstone, the presence of some articulated exoskeletons and little size sorting or fragmentation of disarticulated sclerites suggest that most of the trilobites lived at or near where they were deposited. In grainstone, the trilobites are almost invariably disarticulated and the sclerites commonly are fragmented and size sorted, suggesting transport from shallower environments. Thus, total species diversity in the Holm Dal Formation may have been increased significantly by gravity displacement and redeposition of bioclasts.

Biostratigraphy

Precipitous valley walls make access to the Holm Dal Formation difficult, and collections were obtained only as accessibility permitted (J. S. Peel, personal communication 1981). The most thoroughly collected section of the formation is at the type locality on the east side of Gustav Holm Dal (Fig. 1). Observed ranges of trilobite species in the type section (Fig. 2) suggest the successive appearances of two or more faunules. However, when stratigraphic ranges of species are analyzed from all localities (Figs 2–6), the formation has a fairly uniform fauna throughout, and no biostratigraphic subdivision seems warranted.

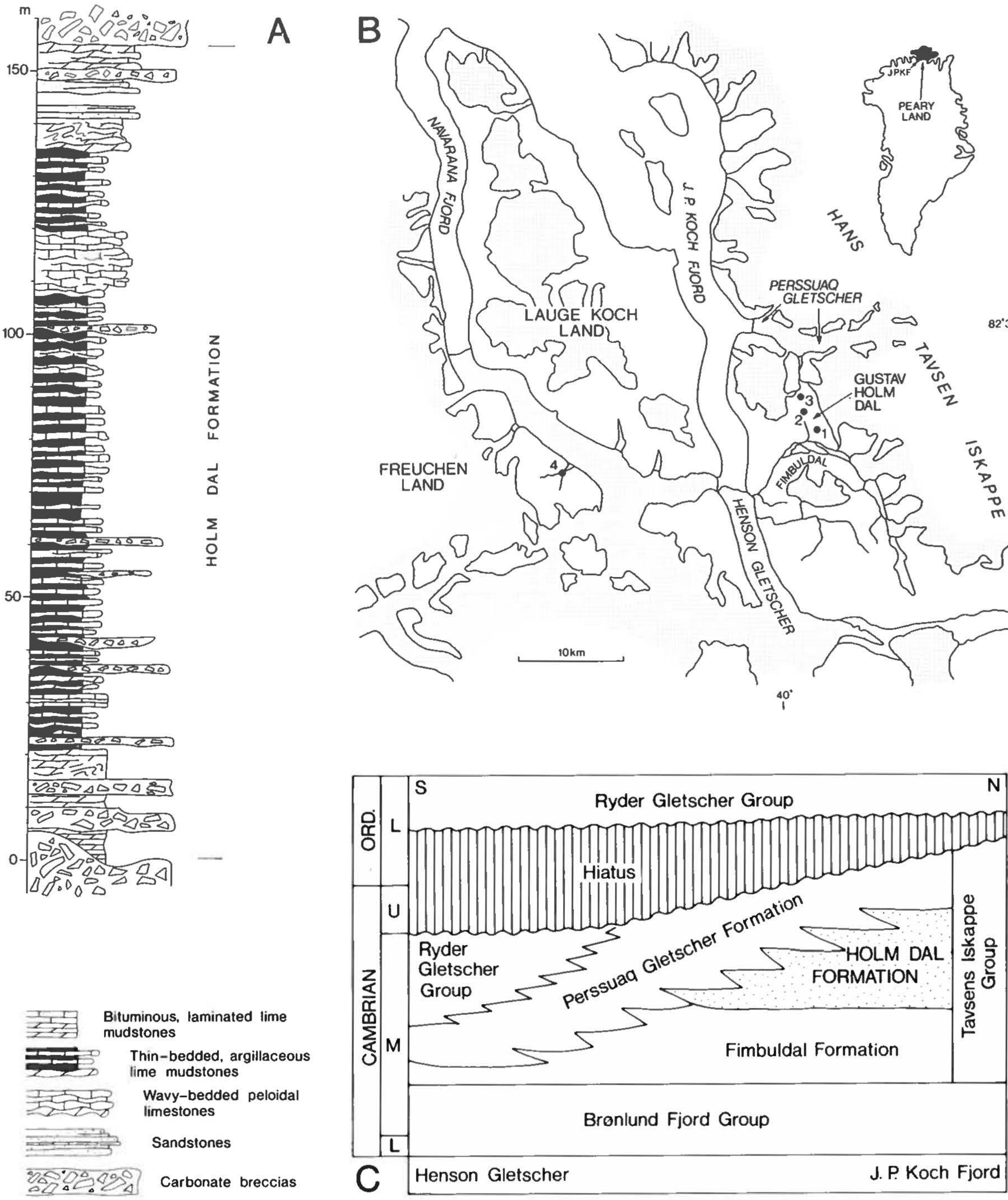


Fig. 1. Derivation of trilobites from the Holm Dal Formation, central North Greenland. A, stratigraphic section through the Holm Dal Formation at its type locality (locality 1 in Fig. 1B; from Ineson, this volume). B, map of the area around Gustav Holm Dal, westernmost Peary Land, central North Greenland. Peary Land and J. P. Koch Fjord (JPKF) are indicated on the small inset map of Greenland. Collection localities within the Holm Dal Formation are numbered 1 to 4: 1, the type section (Fig. 1A) and adjacent area, GGU collections in the sequence 225528–225567 (cf. Figs 2, 3); 2, east side of Gustav Holm Dal, GGU collections 225586, 271403, 271404, 271408, 271414, 271417 (cf. Fig. 4); 3, east side of Gustav Holm Dal, GGU collections 225592–225595 (cf. Fig. 5); 4, south-east Freuchen Land, GGU collections 315007, 315009, 315011–315013 (cf. Fig. 6). C, stratigraphic relationship of the Holm Dal Formation (from Ineson, this volume).

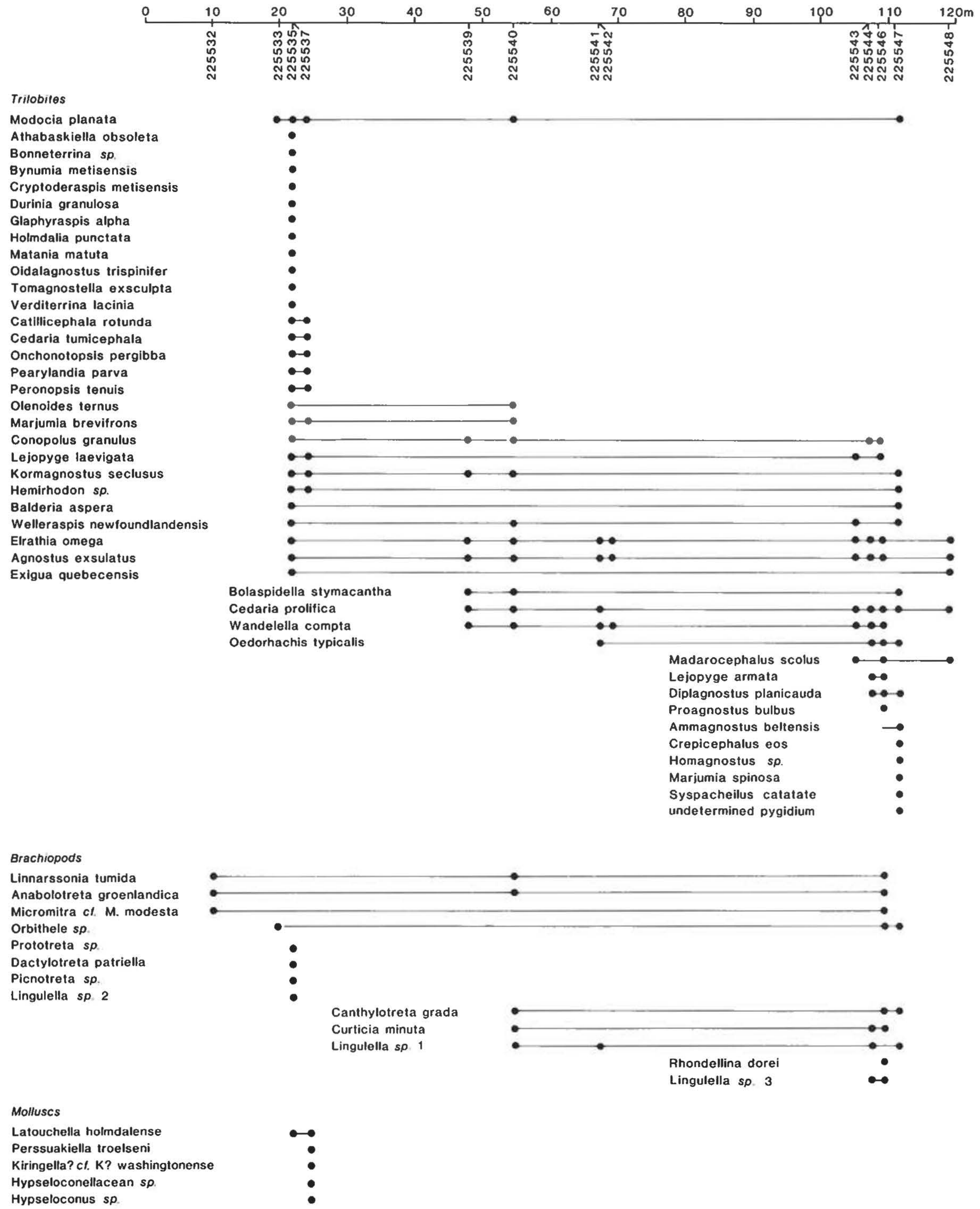


Fig. 2. Stratigraphic distribution of trilobites, brachiopods, and molluscs described from the type section of the Holm Dal Formation (locality 1, Fig. 1B). Six-digit numbers designate GGU collections. The formation is almost 155 metres thick in its type section (Fig. 1A); scale indicates height above base of formation.

	225528	225529	225530	225552	225561	225563	225564	225565	225567
Trilobites									
Bolaspidella stymacantha	●			●	●		●		
Bynumia metisensis	●	●		●	●	●			
Catillicephala rotunda	●	●		●	●	●	●		
Cedaria tumicephala	●	●			●	●	●	●	
Conopolus granulus	●	●		●	●	●			
Crepicephalus eos	●	●		●	●				
Cryptoderaspis metisensis	●				●				
Durinia granulosa	●				●				
Exigua quebecensis	●			●					
Hemirhodon *sp.*	●	●		●	●		●		
Holmdalia punctata	●				●				
Kormagnostus seclusus	●	●		●	●	●	●	●	
Marjumia brevifrons	●	●		●	●		●		
Modocia planata	●	●		●	●	●	●		
Oidalagnostus trispinifer	●	●			●				
Onchonotopsis pergibba	●	●			●	●			
Onchonotopsis physala	●				●				
Pearylandia parva	●	●		●	●	●	●	●	
Proagnostus bulbus	●	●		●	●	●			
Tomagnostella exsculpta	●	●		●			●		
Ammagnostus beltensis		●							
Elrathia omega		●			●	●			
Homagnostus *sp.*		●							
Marjumia spinosa		●				●		●	
Olenoides ternus		●			●		●	●	
Peronopsis tenuis		●				●		●	
Tavsenia ditrema		●		●	●	●	●		
Ankoura *sp.*				●	●	●			
Balderia aspera				●	●				
Blountia *sp.* 1				●					
Lejopyge laevigata				●	●				
Syspacheilus catatate				●	●		●		
Welleraspis newfoundlandensis				●	●			●	
Agelagma quadratum					●				
Blountia *sp.* 2					●				
Hawkinsia? *sp.*					●				
Kingstonia peltata						●		●	
Agnostus exsulatus								●	
Brachiopods									
Acrothelid gen. indet.					●				
Linnarssonia tumida									●
Molluscs									
Stenothecoides groenlandica	●	●		●	●	●	●		
Latouchella holmdalense		●			●	●			
Latouchella pearylandica		●			●				
Kiringella? *cf.* K? washingtonense		?			●	?			
Kiringella *sp.*					●				
Costipelagiella kochi					●				
Euomphalacean (?)					●				
Hypseloconus *sp.*		●				?			
Hyolithids		●	●		●				
Scenella *sp.*			●						

Fig. 3. Species of trilobites, brachiopods, and molluscs in GGU collections from the lowest part of the Holm Dal Formation in the vicinity of its type locality, exclusive of the type section (Fig. 1B, locality 1). Collections are not in stratigraphic sequence.

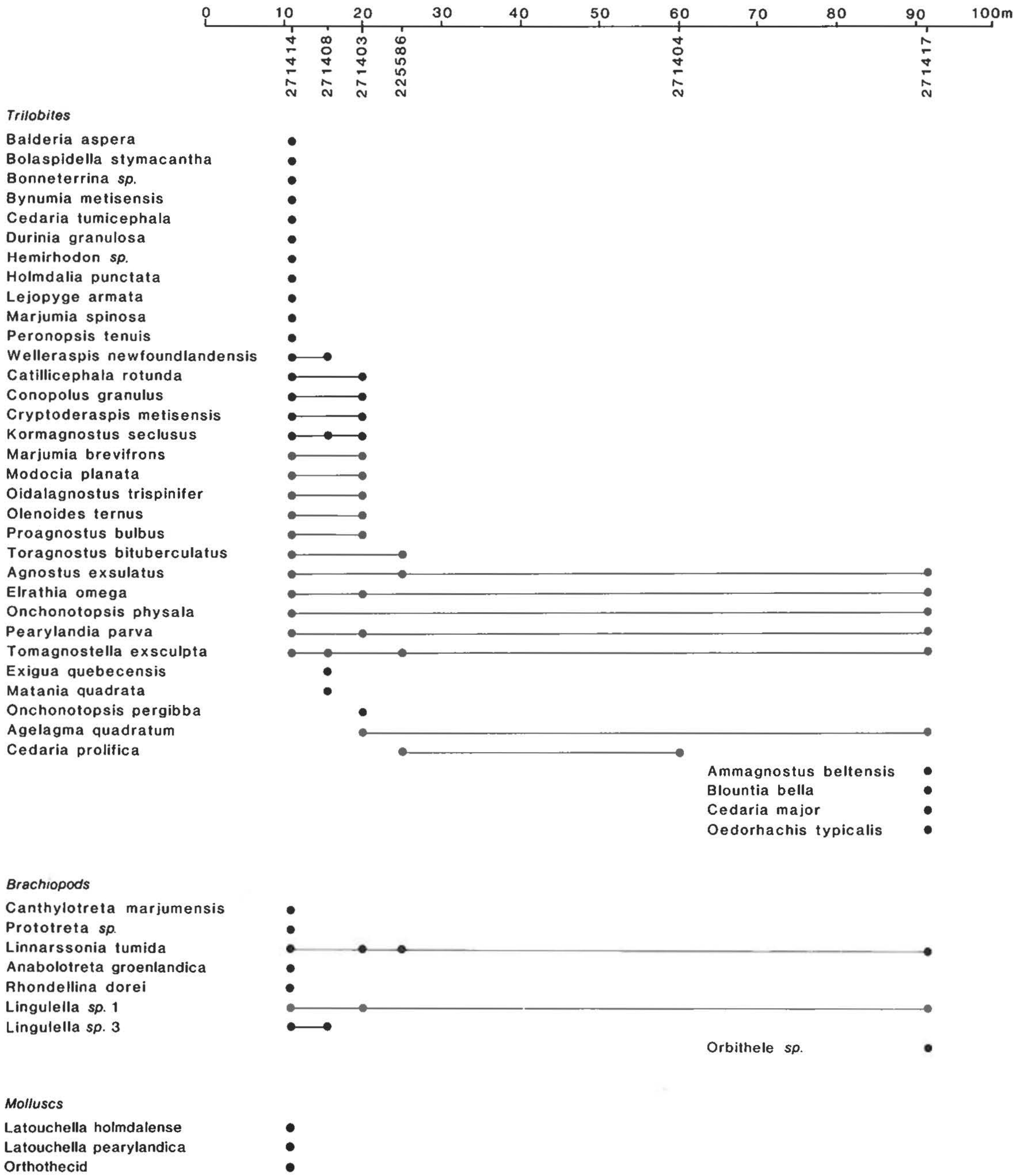


Fig. 4. Stratigraphic distribution of trilobites, brachiopods, and molluscs described from locality 2 (Fig. 1B) of the Holm Dal Formation. Six-digit numbers designate GGU collections. Scale indicates height above base of formation.

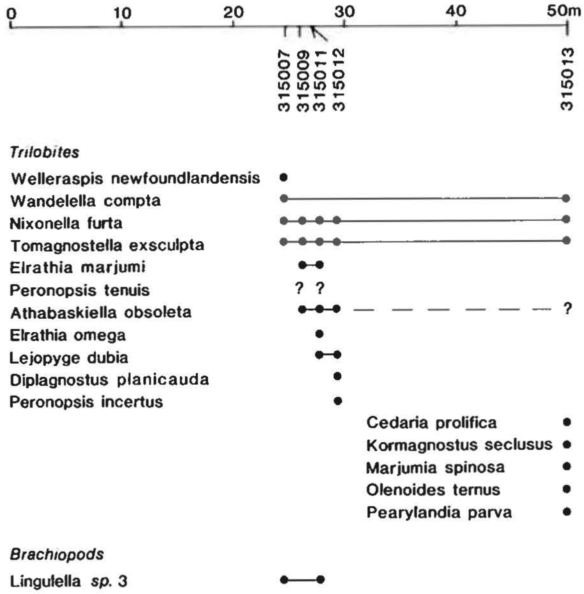


Fig. 6. Stratigraphic distribution of trilobites and brachiopods in GGU collections from locality 4 (Fig. 1B) of the Holm Dal Formation in south-east Freuchen Land. Scale indicates height above the base of the formation.

Representatives of the *Cedaria* Zone are widely known around the remainder of North America and into Missouri and the upper Mississippi Valley. An exhaustive accounting will not be attempted, but some of the more diverse and better documented faunas are from the basal Nolichucky Formation of Tennessee, Alabama, and Georgia (Resser 1938, Rasetti 1965), the basal Bonneterre Dolomite of Missouri (Lochman 1940), part of the Riley Formation in Texas (Palmer 1955), the lower DuNoir Limestone of Wyoming (Lochman & Hu 1960, 1961, 1962), and the basal Pilgrim Formation of Montana (Lochman & Duncan 1944).

Intercontinental correlations

Correlations of the Holm Dal fauna with those outside Laurentia, of necessity, are based almost entirely on agnostoids. Compared to the standard Swedish zonation (Westergård 1946), the Holm Dal fauna correlates most closely with the Zone of *Lejopyge laevigata*, which has been recognized throughout much of Scandinavia (Martinsson 1974).

Correlations with eastern Newfoundland and Great Britain are difficult. Three agnostoid species, *Diplagnostus planicauda, Oidalagnostus trispinifer,* and *Peronopsis tenuis,* are common to the Manuels River Formation and lower Elliot Cove Group of eastern Newfoundland (Hutchinson 1962) and the Holm Dal Formation. These species have long stratigraphic ranges, however, and other agnostoid evidence suggests that some of the occurrences in Newfoundland are older and some are younger than in Greenland. A faunule from the upper Mancetter Grits and Shales in Warwickshire, England (Taylor & Rushton 1972, Rushton 1978), probably correlates with the Holm Dal fauna.

Several agnostoid species from an isolated, 50 m thick outcrop of dark limestone in Mendoza Province, Argentina (Poulsen 1960, with some taxonomic emendation here), indicate close correlation with the Holm Dal fauna. Ramos et al. (1986) have recently noted stratigraphic and faunal similarities between the Precordillera terrane of Argentina (including Mendoza) and the northern Appalachian region of North America. I have examined the Poulsen trilobite collection from Mendoza and have found that the polymeroids have a strong, perhaps total, Laurentian aspect. Further investigation of this fauna is in progress.

Abundant and diverse agnostoid faunas in Australia are well known, especially from work by A. A. Öpik. Nevertheless, generally flat terrain in many areas has made it difficult to obtain reliable information about the stratigraphic distributions of Australian agnostoids. The Holm Dal fauna seems to correlate with faunas from the middle and upper *Lejopyge laevigata, Erediaspis eretes,* and lower *Cyclagnostus quasivespa* zones of Öpik (1967, 1979). Compared with the Swedish standard, I agree with Daily & Jago (1975) that in Australia the Middle – Upper Cambrian boundary seems to fall within Öpik's *C. quasivespa* Zone, and therefore the basal part of his Mindyallan Stage is also Middle Cambrian in age. Presence of the distinctive polymeroid *Agelagma quadratum* in the *Erediaspis eretes* Zone of Australia and the *Lejopyge laevigata* Zone of both Nevada and North Greenland adds support to that conclusion.

Many Cambrian agnostoids have been described from China. They are especially abundant and diverse in dark carbonate lithofacies of the Chiangnan belt in western Hunan Province (Chang 1980) and in the northern Tian Shan of Xinjiang Province (Xiang & Zhang 1985). Agnostoids of the Holm Dal Formation correlate closely with those of the upper Huagiao Formation in western Hunan (Song Yanping & R. A. Robison in prep.) and those of the Akqat and lower Jiangjungou formations in the Tian Shan.

Agnostoid faunas have been described or reported from many areas of the Soviet Union. Of these, the Holm Dal agnostoid fauna correlates most closely with parts or all of the *Lejopyge laevigata* and *Kormagnostus simplex* zones of Ergaliev (1980), as described from the Kyrshabakty section of the Lesser Karatau Range, Kazakhstan. It also seems to correlate closely with the *Lejopyge laevigata – Aldanaspis truncata* Zone of Egorova et al. (1982) in the stratotype of the Mayan Stage of the south-eastern Siberian platform. Available information suggests that the agnostoid-dominated fauna in the Kyrshabakty section of Kazakhstan was deposited in generally deeper water than was the polymeroid-dominated fauna of the upper Mayan Stage in Siberia.

Age of trilobite faunas

Agnostoid and polymeroid trilobites have very different stratigraphic and geographic distribution patterns, which are consistent with inferred basic differences in their modes of life. Agnostoids are found mainly in open-shelf and slope lithofacies. Most were probably pelagic (Robison 1972b, Öpik 1979). In Cambrian deposits of low palaeolatitudes, as in Greenland and North America, almost mutually exclusive polymeroid faunas are present in open-shelf and restricted-shelf lithofacies (Palmer 1973, Robison 1976). Most of those polymeroids were probably benthic. To improve biostratigraphic precision, separate sets of agnostoid and polymeroid biozones have been proposed for some major Middle Cambrian biofacies (Robison 1976). Refinement of an agnostoid zonation is in progress (e.g. Robison 1984).

With regard to agnostoid zonation, faunas of the Holm Dal Formation are restricted to the upper *Lejopyge laevigata* Interval-zone of Robison (1984: 8–9). Of 15 agnostoid species, at least 13 have intercontinental distributions (see Table 3), which enables rather precise biostratigraphic correlations with various open-ocean faunas of the world. Using the biostratigraphic zonation of north-western Europe (Westergård 1946) as a standard, the Holm Dal Formation is latest Middle Cambrian in age.

The diverse polymeroid fauna of the Holm Dal Formation is especially interesting because of the association of several generic indices from the *Bolaspidella, Cedaria,* and *Crepicephalus* biozones as commonly used in North America (e.g. Lochman-Balk & Wilson 1958, Palmer 1979). Nevertheless, based on total generic content and general evolutionary aspect, the Holm Dal fauna is most similar to that of the lower and middle *Cedaria* Zone as documented from many localities in North America.

The *Cedaria* Zone traditionally has been considered to be the lowest Upper Cambrian zone in North America. Compared with the type Cambrian of north-western Europe, agnostoid correlation strongly indicates that the lower and middle *Cedaria* Zone is late Middle Cambrian in age. As a corollary, the lower part of the Dresbachian Stage in North America is also Middle rather than Late Cambrian in age. Such conclusions were previously suggested by Daily & Jago (1975) and were supported by Robison (1984).

Employing the principle of parsimony, polymeroid occurrences in the Holm Dal Formation extend upward the observed stratigraphic ranges of *Athabaskiella, Elrathia,* and *Marjumia.* Similarly, the stratigraphic ranges of *Crepicephalus, Glaphyraspis,* and *Welleraspis* are extended downward.

	225592	225593	225594	225595
Trilobites				
Cedaria prolifica	●	●	●	●
Elrathia omega	●	●	●	●
Modocia planata	●			
Agnostus exsulatus		●	●	●
Lejopyge laevigata				●
Tomagnostella exsculpta				●
Brachiopods				
Linnarssonia tumida	●			●
Anabolotreta groenlandica	●			
Curticia minuta	●			●
Micromitra *cf.* M. modesta	●			
Lingulella *sp.* 1	●	●		●

Fig. 5. Species of trilobites, brachiopods, and molluscs in collections from locality 3 (Fig. 1B) of the Holm Dal Formation. Collections are only placed relative to each other within about the lowest 100 m of the formation. GGU 225592 and 225593 are from near the middle of this interval, 224494 and 225595 are from near the top of this fossiliferous interval.

Correlation within Laurentia

In Greenland, member B of the Cass Fjord Formation in Daugaard-Jensen Land, western North Greenland, contains the only described fauna (Palmer & Peel 1981) that seems to be closely equivalent in age to faunas of the Holm Dal Formation. Minor oolites and, in the upper part, stromatolites in member B of the Cass Fjord suggest much shallower environments than those interpreted for the Holm Dal, which could account for a low species similarity.

Compared to faunas from North America, the Holm Dal Formation shares the greatest number of described trilobite species with the Lévis Formation of Quebec. Individual conglomeratic boulders from the Lévis have yielded a diverse, well-preserved fauna (Rasetti 1946, 1948), but information on stratigraphic context is essentially lacking. Elsewhere in northern Appalachia, poorly preserved faunas in the Rockledge Conglomerate, Skeels Corners Formation, and St. Albans Shale of Vermont (Shaw 1952, 1966a, b) appear to be at least partly correlative with the Holm Dal fauna. In western Newfoundland, a small correlative fauna is known from the Petit Jardin Formation (Lochman 1938) and elements of a *Cedaria* fauna are present in boulders of the Cow Head Conglomerate (e.g. Kindle 1982).

Biogeography

The Holm Dal Formation of North Greenland contains one of the most diverse faunas known from the *Cedaria* Zone. Observed geographic distributions of Holm Dal trilobite taxa are summarized in Table 2. Although detailed evaluation is fraught with problems, general trilobite distribution patterns within the *Cedaria* Zone of Laurentia are evident. Agnostoid correlations also enable some general conclusions to be drawn about intercontinental trilobite distributions during the *Cedaria* biochron. These patterns hold important implications for Cambrian biostratigraphy in general.

Intracontinental trilobite distributions

Several problems hinder analysis of published data pertaining to trilobite distribution in the *Cedaria* Zone of Laurentia. For example, paleoenvironments of samples were diverse and commonly have not been documented, sample sizes are variable, some collecting was biased (especially in favour of polymeroids), taxonomy lacks standardization, and some chronocorrelations may be imprecise. Nevertheless, from a large data base, it is evident that probably at least half of the described polymeroid genera were dispersed around the entire shelf of Laurentia. In comparison, few polymeroid species appear to have more than regional distributions. Of the 43 Holm Dal polymeroid species (Table 2), only 9 (20 percent) are known from the closest region (northern Appalachia), and no more than 3 (7 percent) are known from any other region in North America. Comparison of *Cedaria* faunas from regions within North America indicates values of similar magnitude. It is of interest that of the three polymeroid species *(Agelagma quadratum, Cedaria prolifica,* and *Elrathia marjumi)* common to North Greenland and the Great Basin, each is known in the Great Basin from a different agnostoid zone. Only one Holm Dal polymeroid species *(Cedaria prolifica)* is known from more than 1 of the 8 North American regions listed in Table 2, and that species is long ranging (lower *Cedaria* to upper *Crepicephalus* zones). Important implications of all this for biostratigraphy are that Middle Cambrian zonations based on polymeroid species may be useful on a regional scale but probably will not be applicable on a continental scale. Genus-based polymeroid assemblage-zones may be applicable on a continental scale, but long generic ranges limit precision.

taxa	HD	NA	SA	MV	Mo	Tx	GB	MC	Al	OC
Polymeroid genera	34	21	15	5	7	16	15	14	10	4
percent	-	62	44	15	21	47	44	41	29	12
Polymeroid species	43	9	1	0	0	1	3	0	0	1
percent	-	20	2	0	0	2	7	0	0	2
Agnostoid genera	12	3	5	0	1	2	9	5	4	12
percent	-	25	42	0	8	17	75	42	33	100
Agnostoid species	15	1	3	0	1	1	7	2	1	13
percent	-	7	20	0	7	7	47	13	7	87
All trilobite genera	46	24	20	5	8	18	24	19	14	16
percent	-	52	43	11	17	39	52	41	30	48
All trilobite species	58	10	4	0	1	2	10	2	1	14
percent	-	17	7	0	2	3	17	3	2	24

Table 2. Numbers of trilobite genera and species in the Holm Dal Formation (HD) compared with occurrences of the same taxa elsewhere. Regions, abbreviations, and principal references are: northern Appalachia, including Quebec and western Newfoundland (NA; Lochman 1938; Rasetti 1946, 1948, 1963; Shaw 1952, 1966a, b); southern Appalachia (SA; Resser 1938; Tasch 1951; Rasetti 1965); upper Mississippi Valley (MV; Lochman-Balk & Wilson, 1958); Missouri (Mo; Lochman 1940); Texas (Tx; Wilson 1954; Palmer 1955); Great Basin of Nevada and Utah (GB; Robison 1960, unpublished data); Wyoming, Montana, southern Canadian Rockies (MC; Lochman & Duncan 1944; Lochman & Hu 1960, 1961, 1962); Alaska (Al; Palmer 1968); and other continents (OC, numerous references).

Agnostoid species associated with *Cedaria* faunas, on average, are much more widely distributed than polymeroid species (Table 3). Agnostoid abundance and species diversity tend to be greatest in a lithofacies belt corresponding to the boundary transition from neritic to oceanic environments. In deeper oceanic deposits, agnostoids tend to be sparse and to have low species diversity. In shallow, unrestricted neritic lithofacies, agnostoid diversity commonly drops off to 1 or 2 species. Analogy with ecology of modern plankton suggests that temperature and salinity were important limiting factors. In shallow-water deposits of the *Cedaria* Zone of North America, commonly the only agnostoid is *Kormagnostus seclusus,* which shows exceptional morphological variability, is eurytopic, and is long ranging (*Lejopyge laevigata* to *Glyptagnostus stolidotus* zones). Agnostoid biostratigraphy probably will prove to be most useful in deposits representing the neritic-oceanic transition.

Intercontinental trilobite distributions

Major differences are evident in the intercontinental distributions of Holm Dal trilobite taxa (Table 2, OC). Only 4 of the 34 polymeroid genera *(Agelagma, Bolaspidella, Modocia, Olenoides)* are known without question from outside Laurentia, and only 1 of the 43 species *(Agelagma quadratum).* In marked contrast, all of the 12 Holm Dal agnostoid genera are known outside Laurentia, as are at least 13 of the 15 species (Table 3). The strong continental endemism of the mostly benthic polymeroid genera and species (88 and 97 percent respectively), suggests effective geographic isolation of Laurentia during the Cambrian Period. Except for *Peronopsis incertus,* which is questionably known from China, and one rare species that is left in open nomen-

	NA	Ar	Au	C	SU	Sc	GB	Nf
Agnostus exsulatus		x						
Ammagnostus beltensis	x	x						
Diplagnostus planicauda	o	?	x	x	x	x		x
Homagnostus *sp.*								
Kormagnostus seclusus	x	x	?	?	x			
Lejopyge armata	x		x	x	x	x		
Lejopyge dubia			x	x	x			
Lejopyge laevigata	x		x	x	x	x		
Oedorhachis typicalis	x	x	?					
Oidalagnostus trispinifer			x	x	x	x		x
Peronopsis incertus	x			?				
Peronopsis tenuis		x				x	x	x
Proagnostus bulbus	x		x	x	x			
Tomagnostella exsculpta	o		x	x	x	x	x	
Toragnostus bituberculatus	x			o	x	x		

Table 3. Observed geographic distributions of agnostoid species that are present in the Holm Dal Formation. Abbreviations are: Ar, Argentina; Au, Australia; C, China; GB, Great Britain; NA, North America; Nf, eastern Newfoundland; Sc, Scandinavia; and SU, Soviet Union. Published reports are indicated by an x, unpublished observations by an o, and questionable identifications by a ?. Eastern Newfoundland is listed separately because it is thought to be an exotic terrane, accreted to North America after the Cambrian Period. For references, see synonymy given for each species in the section on systematic descriptions.

clature (*Homagnostus* sp.), all Holm Dal agnostoid genera and species have intercontinental distributions in open-shelf and basinal lithofacies. Such distribution indicates that agnostoids are potentially excellent indices for refining global biostratigraphy in Middle and Upper Cambrian strata.

Systematic descriptions

Terminology. – Morphological terms used are mostly those defined in the Treatise on Invertebrate Paleontology (Harrington et al. 1959). Qualifying terms for polymeroid facial sutures and lateral glabellar furrows are from Henningsmoen (1957: 12–14). Additional terms for agnostoids have been defined by Robison (1964, 1972a, 1984) and Öpik (1967).

One new term is defined here for an iteratively evolved axial structure on the agnostoid pygidium. The feature, *transverse sulcus,* is a transverse depression or groove of variable depth in the posteroaxis (see Fig. 9.7, 8, 10, 11). Although it may superficially resemble a ring furrow, it normally is wider (sag.) than furrows that may bound the two segments of the anteroaxis. Its longitudinal position on the posteroaxis varies from genus to genus and does not seem to necessarily correspond to a metameric boundary. At or near the bottom of the sulcus is usually a secondary median node (e.g. diplagnostids) or a pair of small pits (e.g. *Clavagnostus*). A transverse sulcus is variably developed in such genera as *Aspidagnostus, Clavagnostus, Diplagnostus, Doryagnostus, Goniagnostus, Linguagnostus, Oidalagnostus, Peronopsis, Ptychagnostus,* and *Tomagnostus.* Öpik (1967) applied the terms "rosette" and "knob" to the depression and its small median swelling. Alternative terms are used here, however, because the depression does not have a floral or radial design and "secondary node" has been commonly used for such a median swelling. Moreover, the secondary node may not be centrally located in the sulcus (e.g. *Oidalagnostus*).

Depositories. – All material used in this study is identified by collection or museum numbers. Depositories and their abbreviations for material from Greenland are Geological Survey of Greenland (Grønlands Geologiske Undersøgelse), Copenhagen, GGU, and Geologisk Museum (formerly Mineralogisk Museum), Copenhagen, MGUH.

Phylum Arthropoda
Class Trilobita
Order Agnostida
Family Agnostidae M'Coy

Genus *Agnostus* Brongniart 1822

Type species. – *Entomostracites pisiformis* Wahlenberg 1818, p. 42, pl. 1, fig. 5.

Agnostus exsulatus Poulsen 1960

Fig. 7.4–11

Agnostus exsulatus – Poulsen 1960: 6–7, pl. 1: 3, 4

New material. – More than 100 specimens in GGU 225535, 225539–225544, 225546, 225548, 225565, 225586, 225593–225595, 271414, and 271417.

Remarks. – Numerous specimens from Greenland conform well with Poulsen's (1960) thorough description of *A. exsulatus* from Argentina. As noted by Poulsen, *A. exsulatus* closely resembles *A. pisiformis,* the type species of *Agnostus.* Among the characters that differentiate *A. exsulatus* from *A. pisiformis* are a shorter glabella, a longer pygidial axis, a preglabellar median furrow that weakens anteriorly, a median node that is posterior rather than anterior from the midpoint of the posteroglabella, and slightly more effaced ring furrows on the pygidium.

Occurrence. – *A. exsulatus* now is known from Argentina and North Greenland. Its observed stratigraphic range is restricted to the upper *Lejopyge laevigata* Zone. In the Holm Dal Formation, it is the most common agnostoid in dark lime mudstone, but is present in all lithofacies.

Genus *Homagnostus* Howell 1935b

Type species. – *Agnostus pisiformis* var. *obesus* Belt 1867, p. 295, pl. 12, fig. 4a-d.

Remarks. – The generic diagnosis of Palmer (1960: 62–63) is followed here except for minor emendation to include specimens having a uniformly developed preglabellar median furrow and a pygidial axis that extends to the posterior border furrow.

Homagnostus sp.

Fig. 7.1–3.

Material. – One cephalon and three pygidia in GGU 225529 and one cephalon in GGU 225547.

Remarks. – Rare specimens from Greenland exhibit the distinctive axial structure of *Homagnostus,* including the characteristic inward and forward curvature of the first ring furrow of the pygidium, which partially isolates lateral parts of the first ring. The two cephala are small holaspides having a complete preglabellar median furrow that is narrow and deep. The anteroglabella is small and subcircular. An ill-defined, elongate, median node is near the midpoint of the posteroglabella. The axis on both small and large holaspid pygidia is nearly parallel sided and is longer than usual for the genus, extending to the posterior border furrow. Ring furrows are weakly developed on small pygidia, but are nearly effaced on one large specimen.

The specimens may represent a new species of *Homagnostus.* However, the small sample and the apparent immaturity of most specimens make taxonomic evaluation difficult. Compared with *H. obesus* (Belt), the type species of *Homagnostus,* the specimens from Greenland have a deeper, more uniform preglabellar median furrow, the pygidial axis has weaker ring furrows, and the posteroaxis is longer (cf. Westergård 1947: 3–4, pl. 1: 10, 11; Rushton 1983: 116, pl. 14: 1–10). In length of axis, the pygidia from Greenland resemble those of *H. hoi* (Sun 1924: 28–29, pl. 2: 2a-d) from northern China, but *H. hoi* has a weak, incomplete, preglabellar median furrow. Species assignment of the Greenland specimens is deferred until more taxonomic information is available.

Occurrence. – Rare in lime grainstone from near the base and from about 111 m above the base of the Holm Dal Formation. These specimens may be the oldest known representatives of *Homagnostus* (*H. incertus* Robison 1964, from the *Ptychagnostus punctuosus* Zone having been reassigned to *Peronopsis;* see remarks on *Kormagnostus*).

Family Diplagnostidae Whitehouse

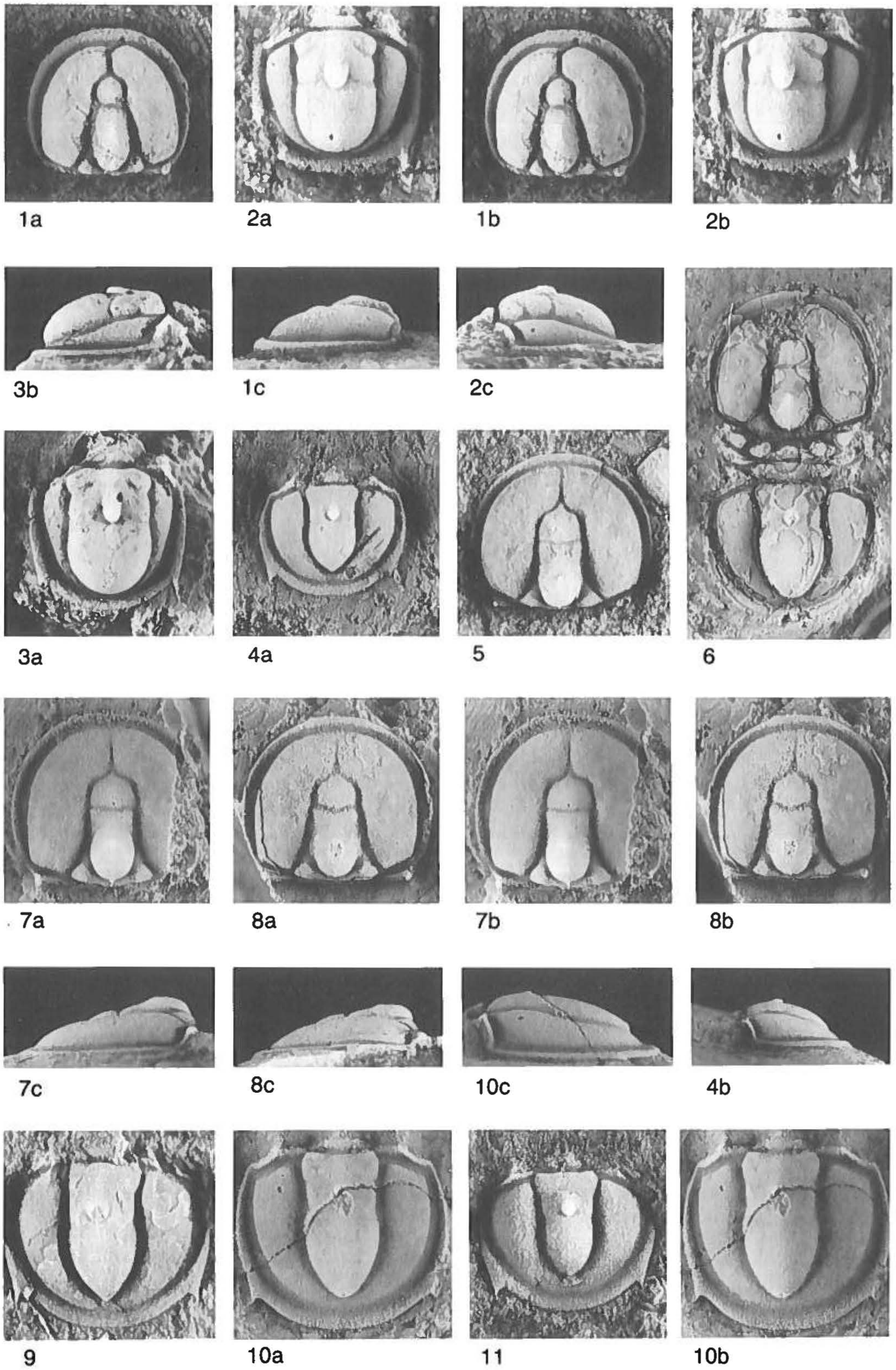
Genus *Diplagnostus* Jaekel 1909

Type species. – *Agnostus planicauda* Angelin 1851, p. 7, pl. 6, fig. 9.

Diplagnostus planicauda (Angelin 1851)

Fig. 8.7, 8

Agnostus planicauda – Angelin 1851: 7, pl. 6: 9; Tullberg 1880: 33, 37, pl. 2: 24; Wallerius 1895: 41, pl. 2: 2; Grönwall 1902: 71–72, pl. 1: 12
Agnostus planicauda vestgothica – Wallerius 1895: 41, pl. 1: 2; Wallerius 1930: 58, fig. 6
Diplagnostus planicauda (Angelin) – Jaekel 1909: 396, fig. 14; Kobayashi 1939a: 140–141; Westergård 1946: 61–62, pl. 8: 22–24; Egorova, Pegel, & Chernysheva in Egorova et al. 1982: 60–61, pl. 21: 1
Enetagnostus humilis – Whitehouse 1936: 91, pl. 8: 17–19
Diplagnostus planicauda vestgothicus (Wallerius) – Kobayashi 1939a: 141; Westergård 1946: 62–63, pl. 8: 25–29; Öpik 1961:70–71, pl. 19: 13a, b
Diplagnostus planicauda bilobatus – Kobayashi 1939a: 141; Westergård 1946: 62, pl. 8: 13–21; Hutchinson 1962: 78, pl. 7: 10–13; Egorova et al. 1963: 61, pl. 7: 5; Chu 1965: 135, pl. 1: 1, 2; Poulsen 1969: 4, fig. 3a, b; Zhou et al. 1977: 108, pl. 36: 7; Egorova, Pegel, & Chernysheva in Egorova et al. 1982: 61, pl. 11: 8, pl. 34: 18, pl. 46: 1; Liu 1982: 290–291, pl. 214: 4
Diplagnostus humilis (Whitehouse) – Kobayashi 1939a: 141; Öpik 1961: 72–73, pl. 19: 15, 16, pl. 20: 2
?Diplagnostus jarillensis – Rusconi 1952: 10–11, pl. 1: 10; Poulsen 1960: 10–11, pl. 1: 9
?Diplagnostus cf. *planicauda vestgothicus* (Wallerius) – Öpik 1961: 71–72, pl. 19: 17, pl. 20: 1, 3
Diplagnostus crassus – Öpik 1967: 126–127, pl. 54: 4
Diplagnostus sp. – Jago 1976: 159–160, pl. 25: 6–9
Diplagnostus planicaudatus (Tullberg) – Yang 1978: 18, pl. 1: 4; Yang 1982: pl. 1: 3, 4
Diplagnostus floralis – Öpik 1979: 40–42, pl. 7: 1–6
Diplagnostus planicauda transversus – Ju in Qiu et al. 1983: 31, pl. 11: 13
Diplagnostus similis – Zhang Quan-zhong in Qiu et al. 1983: 31, pl. 11: 11, 12


1a
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10c
4b
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10a
11
10b

New material. – Four cephala and four pygidia in GGU 225544, ?225546, 225547, and 315012.

Remarks. – New specimens of *D. planicauda* from North Greenland are rare and not well preserved. Although adding no new information on morphology, they do provide data on biostratigraphy and biogeography.

D. planicauda is a distinctive but variable species as documented by Westergård (1946). The cephalon commonly has a medially cleft anterior glabella; the preglabellar furrow varies from well defined to effaced. The posteroglabella bears an elongate median node anterior from its midpoint, and the rear of the glabella varies from rounded to angulate. Genae vary from smooth to moderately scrobiculate. The pygidium is zonate, and has a pair of short posterolateral border spines. A carinate median tubercle usually is evident along the crest of the anteroaxis and may extend slightly onto the posteroaxis. Ring furrows normally are of moderate depth. Flanks of the posteroaxis converge to a pointed end, commonly just short of the collar.

It has been common practice to identify subspecies based on combinations of the variant characters. Westergård (1946: 61), however, noted that "these forms, which mainly differ in the sculpture of the test, are connected by intermediate links and constitute a continuous evolutional series." Another character, width of border furrows, seems to be significantly increased by compression in some kinds of argillaceous matrix. Cited in the synonymy are named specimens that, in my judgment, seem to constitute a single variable species.

Occurrence. – *D. planicauda* is known from Australia, China, Greenland, Scandinavia, the Soviet Union, and questionably Argentina. Specimens also are present in undescribed collections from the western United States (Nevada and Utah). The species has an observed stratigraphic range from near the base of the *Ptychagnostus punctuosus* Zone to near the top of the *Lejopyge laevigata* Zone. In North Greenland, specimens are rare in lime mudstone and grainstone ranging from 27 m to about 111 m above the base of the Holm Dal Formation.

Genus *Oedorhachis* Resser 1938

Oedorhachis – Resser 1938: 49–50; Shimer & Shrock 1944: 601; Howell in Harrington et al. 1959: O185; Poulsen 1960: 12–13; Öpik 1967: 127–128

Type species. – *Oedorhachis typicalis* Resser 1938, p. 50, pl. 10, figs 16, 22, 28.

Emended diagnosis. – Cephalon having short, uncleft anteroglabella. Posteroglabella angulate at rear; median node low, elongate, near midpoint. Genae smooth or weakly scrobiculate; confluent or divided by shallow, incomplete, preglabellar median furrow. Thorax unmodified. Pygidium zonate; posterior border having 2 or 3 short spines. Pygidial axis long, pyriform, reaching posterior border furrow; ring furrows mostly effaced, vestiges may remain near axial furrow; median tubercle moderately large, slightly elongate. Acrolobes usually unconstricted.

Remarks. – Although Palmer (1962: F19) considered *Oedorhachis* to be a junior synonym of *Acmarhachis* Resser 1938, I concur with Öpik (1967: 127–128) that *Oedorhachis* deserves recognition as a separate genus. *Oedorhachis* has an angulate glabellar rear and a zonate pygidial border whereas *Acmarhachis* has a rounded glabellar rear and a simplimarginate pygidium. In form, the pygidial axis of *Oedorhachis* superficially resembles that of *Acmarhachis* but is generally less constricted at the position of the effaced second ring.

Several species have been assigned to *Oedorhachis,* but some of those have subsequently been reassigned to other genera, and some are considered to be synonyms. Only two species, *O. typicalis* Resser 1938, and *O. crenias* Öpik 1979, are here included in the genus. One cephalon appears to be correctly assigned to *O. crenias* (Öpik 1979, pl. 8: 4-lower), but two other cephala having a narrow anteroglabella and rounded glabellar rear (Öpik 1979, pl. 8: 4-upper, 5) probably belong to *Pseudoperonopsis* Harrington 1938.

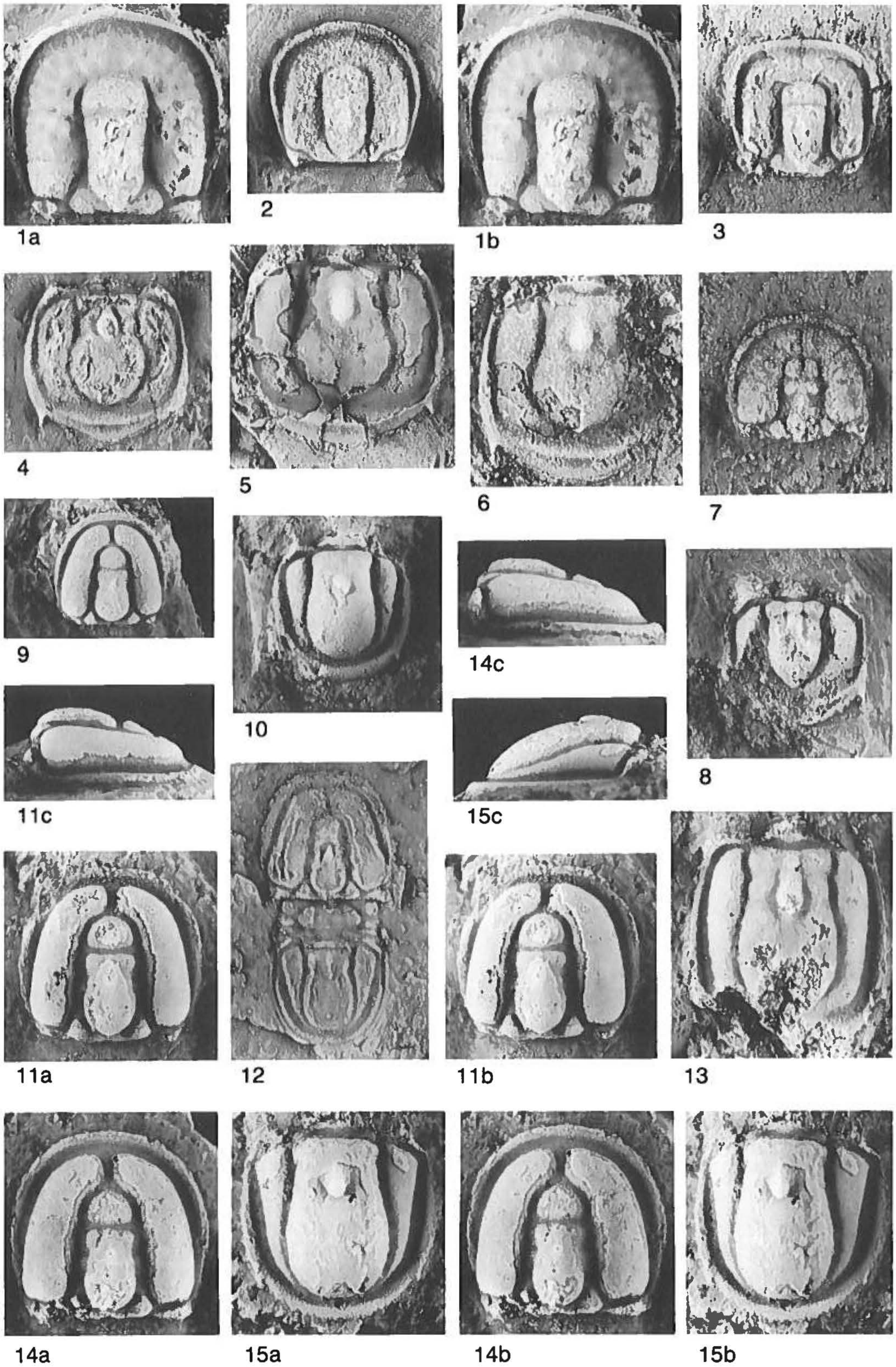
Oedorhachis has an observed stratigraphic range from the *Ptychagnostus punctuosus* to *Lejopyge laevigata* zones. It is known from Argentina, Australia, Greenland, and the United States.

Fig. 7. *Homagnostus* sp. and *Agnostus exsulcatus* Poulsen

1–3. *Homagnostus* sp., all from GGU 225529. 1, 2. Small holaspid cephalon and pygidium in stereo (a, b) and left-lateral (c) views, MGUH 17.104 and 17.105, both X 13.2. 3. Large holaspid pygidium in dorsal (a) and right-lateral (b) views, MGUH 17.106, X 8.8.

4–11. *Agnostus exsulatus* Poulsen, all X 8.8. 4. Pygidium preserved in lime mudstone; dorsal (a) and left-lateral (b) views, MGUH 17.107 from GGU 225546. 5, 9, 11. Cephalon and two pygidia preserved in lime mudstone; dorsal views, MGUH 17.108–17.110, all from GGU 225543. 6. Complete dorsal exoskeleton compressed in lime mudstone, MGUH 17.111 from GGU 225586. 7, 10. Cephalon and pygidium preserved in lime packstone; stereo (a, b) and left-lateral (c) views, MGUH 17.112 and 17.113, both from GGU 271417. 8. Cephalon preserved in lime mudstone; stereo (a, b) and left-lateral (c) views, MGUH 17.114 from GGU 225546.

3*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14a
15a
14b
15b

Oedorhachis typicalis Resser 1938

Fig. 8.1–6

Oedorhachis typicalis – Resser 1938: 50, pl. 10: 16, 22, 28; Shimer & Shrock 1944: 251, fig. 18
not *Oedorhachis typicalis* Resser – Robison 1960: 12–13, pl. 1: 7, 8 [= *Ammagnostus beltensis* (Lochman in Lochman & Duncan 1944)]
Oedorhachis ulrichi – Resser 1938: 50, pl. 10: 29
not *Oedorhachis ulrichi* Resser – Robison 1960: 13, pl. 1: 9 [= *Triadaspis bigeneris* Öpik 1967]
Oedorhachis australis – Poulsen 1960: 13, pl. 1: 8
Acmarhachis ulrichi (Resser) – Palmer 1962: F19
?*Oedorhachis tridens* – Öpik 1967: 128, pl. 54: 5

New material. – Fifteen cephala and 10 pygidia in 225541, 225544, 225546, 225547, and 271417.

Emended diagnosis. – Cephalon subquadrate to subcircular. Glabella expands slightly toward anterior; transglabellar furrow (F3) shallow; anteroglabella short, wide. Basal lobes large, simple. During late holaspid ontogeny anterior cephalic margin may become broadly ogiviform and genae may become weakly scrobiculate.

Pygidium subcircular. Posteroaxis well rounded at rear. Collar appears during mid-holaspid ontogeny, and crescentic gap between collar and posterior border closes during late holaspid ontogeny. Posterolateral border having pair of short spines; median border spine may be present, especially in very large holaspides.

Remarks. – *O. typicalis* differs from *O. crenias*, its probable ancestor, by having a forwardly expanding glabella, resulting in a noticeably wider anteroglabella. On the pygidium, the posteroaxis of *O. typicalis* is more swollen, and the rear end is well rounded rather than pointed.

O. tridens Öpik 1967, is a questionable synonym of *O. typicalis*. The one figured pygidium appears to be an unusually large holaspid, which Öpik (1967) differentiated from *O. typicalis* by its median border spine and absence of a collar. During late holaspid ontogeny of other diplagnostids (see *Oidalagnostus trispinifer*) the gap between the collar and border closes and the two structures merge. Also, presence of a median border spine is variable, but is more common during late ontogeny. Thus, the characters used to differentiate the large holotype of *O. tridens* are not different from those to be expected in a late holaspid of *O. typicalis*.

In *O. typicalis* from Alabama and Tennessee (Resser 1938), a median spine is rarely present on the border of otherwise similar pygidia. All available specimens from Greenland lack a median spine. However, one unusually large cephalon (Fig. 8.1) has a broadly pointed anterior margin, which probably corresponds to the presence of a median spine on its pygidium, being juxtaposed during enrollment. Because of these features, and because the presence of a median spine on the pygidial border is variable in at least one other diplagnostid *(Oidalagnostus),* I do not attribute taxonomic significance to that character in species of *Oedorhachis*.

Occurrence. – *O. typicalis* is known from Argentina, ?Australia, Greenland, and the United States. All specimens are from the *Lejopyge laevigata* Zone. In Greenland, the species is rare to common in dark lime mudstone and rare in packstone and grainstone. It has an observed range from 22 to 111 m above the base of the Holm Dal Formation.

Genus *Oidalagnostus* Westergård 1946

Oidalagnostus – Westergård 1946: 65; Hupé 1953: 121; Howell in Harrington et al. 1959: O175; Pokrovskaya in Chernysheva 1960: 57; Lu et al. 1965: 24; Öpik 1967: 134; Lu in Lu et al. 1974: 80–81; Jago 1976: 160–161.
Ovalagnostus – Lu in Lu et al. 1974, pp. 81–82; Qiu et al. 1983, p. 32.
Tasagnostus – Jago 1976, p. 161

Type species. – *Oidalagnostus trispinifer* Westergård 1946, pp. 65–67, pl. 9, figs 4–7.

Fig. 8. *Oedorhachis typicalis* Resser, *Diplagnostus planicauda* (Angelin) and *Proagnostus bulbus* (Butts)

1–6. *Oedorhachis typicalis* Resser, all X 8.8. 1. Large cephalon with broadly ogiviform anterior margin and weak genal scrobicules, in stereo (a, b) view, MGUH 17.115 from GGU 271417. 2. Subcircular cephalon, MGUH 17.116 from GGU 225544. 3. Subquadrate cephalon, MGUH 17.117 from GGU 225541. 4. Pygidium compressed in lime mudstone, MGUH 17.118 from GGU 225544. 5, 6. Fragmentary larger pygidia in lime mudstone, MGUH 17.119 and 17.120, both from GGU 225546.
7–8. *Diplagnostus planicauda* (Angelin), X 8.8. 7. Cephalon compressed in lime mudstone, MGHU 17.121 from GGU 225544. 8. Fragmentary pygidium, MGUH 17.122 from GGU 315012.
9–15. *Proagnostus bulbus* Butts, all X 8.8. 9. Small holaspid cephalon, MGUH 17.123 from 271414. 10. Small holaspid pygidium, MGUH 17.124 from 225563. 11, 14. Larger cephala in stereo (a, b) and right-lateral (c) views, MGUH 17.125 and 17.126 from GGU 271414 and 225561, respectively. 12. Lectotype, strongly compressed dorsal exoskeleton in pale-brown shale of the Conasauga Formation, Cedar Bluff, Alabama; U. S. National Museum of Natural History no. 94867. The median node on the posteroglabella seems to have been accentuated by compression. The second thoracic segment appears to have been displaced over the anterior pygidium, causing secondary indentation of a transverse groove near the front of the anteroaxis but not on the pleural lobes. 13. Fragmentary large pygidium, MGUH 17.127 from 225563. 15. Large pygidium in stereo (a, b) and right-lateral (c) views, MGUH 17.128 from GGU 225563.

Emended diagnosis. – Cephalon having angulate glabellar rear. Anteroglabella short, uncleft. Median node elongate and anterior from midpoint of posteroglabella. Preglabellar median furrow weak or absent, commonly incomplete. Gena, as well as pleural field of pygidium, smooth or with weak, irregular, scrobicular pits.

Labrum subovate with narrow anterolateral borders. Base lacking fenestrules.

Pygidium zonate. Pygidial collar near or merged with posterior border; crest of collar commonly with pair of central knobs. Axis long, reaching collar, expanded at posterior end. Anteroaxis having elongate median tubercle, best developed on second ring. Posteroaxis unequally divided by deep transverse sulcus; shorter anterior portion bulging laterally, interrupting course of axial furrow; lateral bulges vary in tumescence and may be isolated by shallow furrows. Secondary median node on front slope of transverse sulcus. Swelling may develop on posterior part of pleural field in oblique backward alignment with lateral bulge of posteroaxis. Border having 2 or 3 short spines.

Remarks. – The cephalon of *Oidalagnostus* differs little from that of other diplagnostids, but the pygidium is distinctive. An elongate pygidial axis reaches the pygidial collar and the back end of the axis is unusually large for a diplagnostid. A prominent transverse sulcus (see Terminology, above) crossing the front part of the posteroaxis should not be confused with a true ring furrow.

Specimens here assigned or reassigned to *Oidalagnostus* are unusually variable; some changes being phylogenetic and some ontogenetic, or both. Early forms have two pygidial spines and later forms add a median spine. Presence of a median spine is variable within single collections from Greenland, seemingly being added during holaspid ontogeny. Swelling of distinctive lateral bulges on the posteroaxis, and then development of swellings on the posterior pleural fields, is unique among diplagnostids. Weak scrobicular pits on genae and pleural fields seem to appear during phylogeny and generally tend to be best developed on large holaspides. The two knobs and intervening depression on the pygidial collar are progressively accentuated during phylogeny. Among specimens from Greenland, a narrow crescentic depression between the pygidial collar and the narrow border is eliminated during ontogeny as the collar and border are merged (cf. Fig. 9.7, 8, 10, 11). Some synonymies proposed here are based, at least in part, on these observations.

Oidalagnostus changi Lu in Wang 1964, was designated as the type species of *Ovalagnostus* Lu in Lu et al. 1974. The holotype and only illustrated specimen of *O. changi* appears to be dorsoventrally flattened and laterally compressed in shale. A more rounded cephalon, a longer posteroaxis behind the transverse sulcus, and a lack of swellings on the posterior pleural fields were cited by Lu (in Lu et al. 1974: 82) as characters differentiating *Ovalagnostus* from *Oidalagnostus*. Compared with other specimens variably oriented and deformed in shale (e.g. Jago 1976, pls 25, 26), all of the differential characters cited for *Ovalagnostus* seem to be the result of taphonomic alteration. Therefore, I consider *Ovalagnostus* to be a subjective junior synonym of *Oidalagnostus*.

Previous definitions of *Oidalagnostus* have emphasized the presence of three border spines on the pygidium. Jago (1976) named *Tasagnostus* and differentiated it from *Oidalagnostus* by the presence of only two border spines. Because of close similarity in other characters, and because the presence of a median spine now seems to be of minor taxonomic value in this group, I consider *Tasagnostus* to be a subjective junior synonym of *Oidalagnostus*.

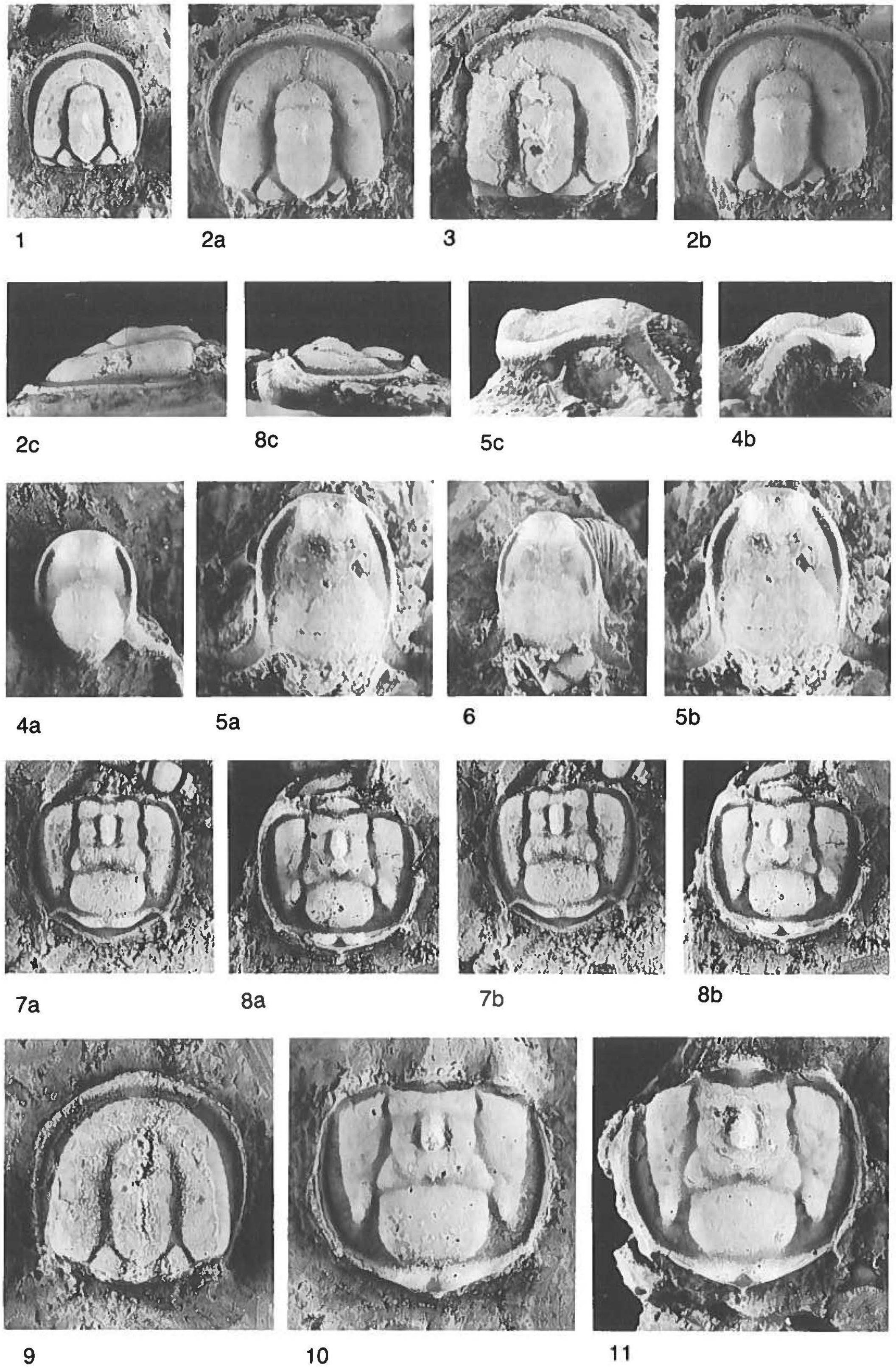
Oidalagnostus and *Dolichagnostus* Pokrovskaya 1958, appear to be closely related. *D. admirabilis* Pokrovskaya 1958, the type species of *Dolichagnostus*, lacks a pygidial collar but closely resembles *O. debori* (Jago 1976) in axial structure.

Species presently assigned to *Oidalagnostus* include *O. debori* and *O. trispinifer*. The taxonomic status of *O. changi* Lu and *O. compani* (Jago 1976) is uncertain because of poor preservation of type specimens. However, I consider both of those species to be questionable synonyms of *O. trispinifer*. *Oidalagnostus? dubius* Westergård 1946 (pl. 9: 8), appears to be more closely related to *Dolichagnostus* than to *Oidalagnostus*.

Specimens referable to *Oidalagnostus* have been described from Sweden, Australia, Canada, China, and the Soviet Union. Specimens from North Greenland are described here. The genus has an observed stratigraphic range from the upper Middle Cambrian (*Lejopyge laevigata* Zone) to the lower Upper Cambrian (*Glyptagnostus stolidotus* Zone).

Fig. 9. *Oidalagnostus trispinifer* Westergård.

1–11. *Oidalagnostus trispinifer* Westergård. 1. Small holaspid cephalon with medial swelling on anterior border, MGUH 17.129 from GGU 271414, X 5.5. 2. Moderately large holaspid cephalon with weak scrobicular pits on genae; stereo (a, b) and left-lateral (c) views, MGUH 17.130 from GGU 225561, X 5.5. 3. Fragmentary cephalon, MGUH 17.131 from 225561, X 5.5. 4. Labrum in ventral (a) and right-lateral (b) views; MGUH 17.132 from GGU 225535, X 8.8. 5. Labrum in stereo (a, b) and left-lateral (c) views; MGUH 17.133 from GGU 225528, X 8.8. 6. Labrum in ventral view, MGUH 17.134 from GGU 271414, X 8.8. 7. Intermediate holaspid pygidium with only two border spines and separated collar and border; stereo (a, b) view, MGUH 17.135 from GGU 225529, X 5.5. 8. Intermediate holaspid pygidium with three border spines and nearly merged collar and border; stereo (a, b) and left-lateral (c) views, MGUH 17.136 from GGU 225528, X 5.5. 9. Large cephalon, thinly encrusted with secondary calcite, MGUH 17.137 from GGU 225561, X 5.5. 10, 11. Large three-spined pygidia, each with merged collar and border; MGUH 17.138 and 17.139, both from GGU 225561, both X 5.5.


1
2a
3
2b
2c
8c
5c
4b
4a
5a
6
5b
7a
8a
7b
8b
9
10
11

Oidalagnostus trispinifer Westergård 1946

Fig. 9.1–11

Agnostus fallax ferox Tullberg – Wallerius 1895 (in part): 43, pl. 9: 4
Oidalagnostus trispinifer – Westergård 1946: 65–67, pl. 9: 4–7; Howell in Harrington et al. 1959: fig. 114.3a, b; Pokrovskaya in Chernysheva 1960: pl. 1: 6, 7; Rosova 1964: 22–23, pl. 13: 1, 2; Jago 1976: 160, pl. 24: 15, 16; Ergaliev 1980: pl. 3: 10
Oidalagnostus cf. *O. trispinifer* Westergård – Hutchinson 1962 (in part): 80, pl. 7: 17–19 (not 20)
?*Oidalagnostus changi* – Lu in Wang 1964: 30, pl. 3: 11; Lu et al. 1965: 24, pl. 1: 26
Oidalagnostus personatus – Öpik 1967: 136–137, pl. 54: 7–9, text-fig. 39
Oidalagnostus tienshanicus – Lu in Lu et al. 1974: 81, pl. 1: 5–7
?*Ovalagnostus changi* (Lu) – Lu in Lu et al. 1974: 82–83, pl. 1: 8; Qiu et al. 1983: pl. 11: 17
?*Tasagnostus compani* – Jago 1976: 165–166, pl. 25: 10–16
Ovalagnostus bispiniformis – Zhou & Yang in Zhou et al. 1977 (in part): 109, pl. 36: 9 (not 8); Yang 1978 (in part): 19, pl. 1: 7 (not 6)
Oidalagnostus bispiniformis (Zhou & Yang) – Liu 1982 (in part): 291, pl. 207: 9 (not 10)

New material. – At least 5 cephala, 8 labra, and 12 pygidia in GGU 225528, 225529, 225535, 225561, 271403, and 271414.

Emended diagnosis. – Posterior end of pygidial axis bluntly rounded. Pygidial collar well developed, laterally sinuous, ends merging into bases of posterolateral border spines; central knobs prominent. Swellings generally developed on sides of posteroaxis in front of transverse sulcus and on posterior pleural fields. Pygidial margin usually trispinose in large holaspides. During holaspid ontogeny, narrow depressed area between pygidial border and collar gradually disappears as those two structures merge. Cephalic border may have slight medial swelling or short anterior prong.

Description of labrum. – Outline subovate in ventral view. Border furrows well developed anterolaterally, weakening and disappearing anteromedially and posterolaterally. Lateral borders highly convex; width narrow, fairly uniform. Apical boss broadly elliptical, tumid, weakly subdivided by medial depression. Transverse furrow broad, ill defined; widening laterally into shallow deltoid depressions adjacent to border furrows. Base broadly convex, whole (i.e., lacking fenestrules). Anterior wings long, slender, narrowing distally. Posterior wings poorly preserved; apparently long, slender.

Remarks. – Several specimens from Greenland closely resemble those from Sweden that Westergård (1946) described as *O. trispinifer*. Contrary to Westergård, however, and as correctly noted by Öpik (1967: 134), *O. trispinifer* does not possess a pseudolobe on the pygidium.

Species assigned to either *Oidalagnostus* or *Ovalagnostus* have been based on few specimens, and some of the specimens are poorly preserved. Several specimens from Greenland are fairly well preserved, but show more morphological variation than is usual in agnostoid species. Based on that observed variation, I consider *Oidalagnostus personatus* Öpik 1967, *Oidalagnostus tienshanicus* Lu in Lu et al. 1974, and *Ovalagnostus bispiniformis* Zhou & Yang in Yang 1978 (in part), to be junior synonyms of *O. trispinifer*. Type specimens of *Oidalagnostus changi* Lu in Wang 1964, and *Tasagnostus compani* Jago 1976, are poorly preserved in shale, which makes evaluation difficult. Nevertheless, I also consider those two species to be questionable synonyms of *O. trispinifer*. The cephalon assigned to *O. bispiniformis* by Zhou & Yang (in Zhou et al. 1977, pl. 36: 8) has a deep preglabellar median furrow and appears to represent *Proagnostus* Butts 1926, rather than *Oidalagnostus*.

O. trispinifer differs from *O. debori* by having a more expanded and blunter posterior axis on the pygidium. In large holaspides, *O. trispinifer* usually has 3 rather than 2 border spines. Swellings on the anteroaxis and pleural fields generally are better developed, and the pygidial collar is more complex. A probably higher first stratigraphic appearance, in combination with these seemingly more advanced characters, suggest that *O. trispinifer* was derived from *O. debori*.

On the basis of size and association of sclerites in multiple collections, a distinctive agnostoid labrum (Fig. 9.4–6) is assigned to *O. trispinifer*. It differs from some previously described agnostoid labra (e.g. Robison 1972a, Ritterbush 1983) by being subovate rather than subtriangular in ventral view. Also, it is unusual in having well-defined lateral borders.

In exceptionally well-preserved specimens of *Agnostus pisiformis* Müller & Walossek (1987) have shown that the labrum is a prominent ventral structure. When the agnostid is in an enrolled condition, the labrum projects far into a ventral concavity of the pygidial axis. Also, during enrollment the position of the anterior end of the labrum approximately corresponds to the position of the posterior end of the pygidial axis. Therefore, based on the anatomy of *A. pisiformis*, I suggest that the posteroaxis of *O. trispinifer* is abnormally swollen to accommodate the unusually large labrum during enrollment. Comparison of profile views suggests that the transverse sulcus of the posterior pygidium (Fig. 9.8c) and the transverse furrow of the labrum (Fig. 9.4b, 5c) are complementary, coaptive structures that corresponded in position during enrollment.

Occurrence. – As here revised, *O. trispinifer* has wide geographic distribution, being known from Sweden, Australia, Canada (eastern Newfoundland), China, the Soviet Union, and Greenland. It usually is associated with faunas of the *Lejopyge laevigata* Zone, but ranges from there into the *Glyptagnostus stolidotus* Zone of Tasmania (Öpik 1967: 134). In North Greenland, *O. trispinifer* is most common in lime grainstone and is rare in lime wackestone, all from the basal 22 m of the Holm Dal Formation.

Genus *Proagnostus* Butts 1926

Proagnostus – Butts 1926: 76; Kobayashi 1939b: 578; Shimer & Shrock 1944: 601; Palmer 1962: F13
Sulcatagnostus – Kobayashi 1937: 451; 1939a: 159
Agnostascus – Öpik 1967: 147
Pseudagnostus (Sulcatagnostus) Kobayashi – Rushton in Taylor & Rushton 1972: 20; Shergold 1977: 89–90
Formosagnostus – Ergaliev 1980: 92
Kunshanagnostus – Qian & Zhou 1984: 173

Type species. – *Proagnostus bulbus* Butts 1926 (in part), p. 76, pl. 9, fig. 12 (not 11).

Emended diagnosis. – Cephalon having deep axial and preglabellar median furrows. Acrolobe unconstricted or constricted. Glabella bipartite; anteroglabella uncleft; posteroglabella rounded at rear, F2 weakly developed abaxially, carinate median node anterior from midpoint. Genae smooth or very weakly scrobiculate.

Thorax unmodified.

Pygidium simplimarginate or weakly zonate. Acrolobe constricted. Axial furrow deep, narrowing posteriorly. Axis long, commonly pyriform, rarely subcylindrical, extending to border furrow. Ring furrows effaced or only weakly developed. Median tubercle elongate, usually most tumid at rear of second ring. Posteroaxis swollen, greatest width about midlength, broadly rounded at rear; pleural fields correspondingly reduced in width, especially at rear. Border having 2 or 3 short spines.

Remarks. – The type species of *Proagnostus*, by monotypy, is *P. bulbus* Butts 1926. As noted in a concise review by Rushton (1978: 260), some of which is paraphrased here, the concept of *Proagnostus* is unsettled because of confusion about the primary types of *P. bulbus*. That binomen was applied to two specimens that Butts (1926) figured but did not describe. In my opinion, one is a *Baltagnostus*-like pygidium (according to Rushton, *Peronopsis*-like). The other is a complete diplagnostid exoskeleton. In 1938, Resser refigured Butts' complete specimen of *P. bulbus*. In addition, Resser figured a complete specimen of *Homagnostus*, which he mistakenly referred to as the "holotype" of *P. bulbus*. Rushton (1978) further noted that, in accord with the International Code of Zoological Nomenclature, Article 11, the name *Proagnostus bulbus* is available from 1926, but the "holotype" designated by Resser was not mentioned by Butts and is not even available for selection as the lectotype of P. bulbus. In order to stabilize the concept of *Proagnostus*, I here select the complete specimen figured by Butts (refigured here, Fig. 8 .12) to be the lectotype of *Proagnostus bulbus*. Based on characters of that lectotype, I consider *Sulcatagnostus* Kobayashi 1937, *Agnostascus* Öpik 1967, *Formosagnostus* Ergaliev 1980, and *Kunshanagnostus* Qian & Zhou 1984, to be subjective junior synonyms of *Proagnostus*.

As here diagnosed, *Proagnostus* is a diplagnostid that is closely similar to *Pseudagnostus* Jaekel 1909. There is no cogent evidence, however, to indicate that *Proagnostus* has a deuterolobe (= pseudolobe), which is a taxonomically important character of *Pseudagnostus*. The observed stratigraphic ranges of *Proagnostus* and *Pseudagnostus* partially overlap, with *Proagnostus* appearing slightly lower than *Pseudagnostus*, and *Pseudagnostus* ranging considerably higher than *Proagnostus*. Representatives of the two genera seem to be closely related, but the ancestral source of each genus is unclear. Based on comparative morphology of the earliest known species of each genus (*Proagnostus bulbus* and *Pseudagnostus bulgosus* Öpik 1967), it seems more likely that they share a common ancestor than that the ancestral species of *Pseudagnostus* was derived from a species of *Proagnostus* by development of a deuterolobe.

After review of available literature, many widely distributed specimens, which were originally described under several different generic names, are reassigned here to *Proagnostus*. Most of the specimens appear to represent *P. bulbus*. Rare specimens represent *P. securiger* (Lake 1906) or *P. zonatus* (Öpik 1967), and the specific assignment of some is questionable or indeterminate.

P. bulbus and *P. securiger* comprise an inferred evolutionary lineage in which early pygidia have two border spines and later ones have three. This evolution in spinosity is similar to that shown by species of *Oidalagnostus* (as here revised).

As emended, *Proagnostus* is known from Australia, China, England, Greenland, the Soviet Union, and the United States. It has an observed stratigraphic range from the upper *Lejopyge laevigata* Zone to at least the *Glyptagnostus reticulatus* Zone.

Proagnostus bulbus Butts 1926

Fig. 8.9–15

Proagnostus bulbus – Butts 1926 (in part): 76, pl. 9: 12 (not 11); Resser 1938 (in part): 48, pl. 10: 17 (not 21); Shimer & Shrock 1944 (in part): pl. 251: 4 (not 3)

?*Kormagnostus speciosus* – Resser 1938: 49, pl. 10: 10
Homagnostus bulbus (Butts) – Kobayashi 1939a: 163; ?Romanenko 1977: 164, pl. 23: 1
?*Proagnostus speciosus* (Resser) – Lochman 1940: 24; Palmer 1962: F13
Agnostus aff. *Agnostus pisiformis* Linnaeus – Öpik 1967 (in part): 96–97, pl. 57: 13 (not 12)
Agnostus artilimbatus – Öpik 1967 (in part): 97–98, pl. 57: 10 (not 11)
Agnostascus gravis – Öpik 1967: 147–148, pl. 61: 1–4
Agnostascus sp. nov. aff. *gravis* – Öpik 1967: 148–149, pl. 61: 5, 6
Sulcatagnostus quruqensis – Lu in Lu et al. 1974: 84, pl. 1: 10
Ovalagnostus bispiniformis – Zhou & Yang in Zhou et al. 1977 (in part): 109: pl. 36: 8 (not 9); Yang 1978: 19, pl. 1: 6 (not 7)
Kormagnostus speciosus Resser – Yang 1978: 30, pl. 1: 23, 24
Kormagnostus antiquus Rasetti – Yang 1978: 31, pl. 1: fig. 25
Agnostascus orientalis – Ergaliev 1980: 84–85, pl. 5: 5–7; Xiang & Zhang 1985: 83–84, pl. 7: 6–18
Formosagnostus formosus – Ergaliev 1980: 92–93, pl. 5: 10, 11, 13, pl. 8: 12, 13
?*Homagnostus captiosus* (Lazarenko) – Yang 1982: 300, pl. 1: 1
Oidalagnostus bispiniformis (Zhou & Yang) – Liu 1982 (in part): 291, pl. 207: 10 (not 9)
Kormagnostus speciosus Resser – Liu 1982: 296, pl. 212: 6
Agnostascus sp. – Qian & Zhou 1984: 172–173, pl. 1: 7b
Kunshanagostus kunshanensis – Qian & Zhou 1984: 173–174, pl. 1: 4–6, 7a
Homagnostus sp. – Xiang & Zhang 1985: 66–67, pl. 7: 19

Lectotype. – The specimen (USNM 94867) figured by Butts (1926, pl. 9: 12) is here selected as the lectotype of *Proagnostus bulbus*.

New material. – Thirteen cephala and 5 pygidia in GGU 225528, 225529, 225546, 225552, 225561, 225563, 271403, and 271414.

Diagnosis. – *Proagnostus* having simplimarginate pygidium with pair of small porterolateral border spines; medial border spine lacking. Genae smooth.

Remarks. – *P. bulbus* is the oldest known species of *Proagnostus*. It can be differentiated from *P. securiger* (Lake) by its smooth genae and lack of a medial border spine on the pygidium. It differs from *P. zonatus* (Öpik) by having a simplimarginate rather than a weakly zonate pygidium, a less elongate median tubercle, and lack of a sulcus on the posteroaxis.

Occurrence. – As revised, *P. bulbus* is known from Australia, China, Greenland, the Soviet Union, and the United States. It is common in the *Lejopyge laevigata* Zone and ranges at least into the lowermost Upper Cambrian. In Greenland, specimens are mostly preserved in lime grainstone, are rare in lime mudstone and wackestone, and range through the lower 110 m of the Holm Dal Formation.

Family Peronopsidae Westergård

Genus *Ammagnostus* Öpik 1967

Ammagnostus – Öpik 1967: 137–139
Agnostoglossa – Öpik 1967: 145
Glyptagnostus (Lispagnostus) – Öpik 1967: 169

Type species. – *Ammagnostus psammius* Öpik 1967, pp. 139–141, pl. 55, fig. 3; pl. 66, figs 1–4.

Emended diagnosis. – Cephalon subcircular to subquadrate. Glabella bipartite, rounded at rear; median node near middle of posteroglabella. Basal lobes simple. Genae smooth, anteriorly confluent. Pygidium subcircular to ovoid, simplimarginate. Pygidial axis broad, subcylindrical to weakly pyriform, reaching posterior border furrow; ring furrows mostly effaced; median tubercle small. Acrolobe unconstricted to weakly constricted on cephalon, unconstricted to constricted on pygidium. Border furrow moderately wide on cephalon and pygidium. Border of pygidium having pair of small posterolateral spines.

Remarks. – Öpik (1967: 138) assumed that the secondary node on the agnostoid pygidial axis "marks the rear of the visceral axial lobe." He further concluded that the forward position of the node in *Ammagnostus*, as he defined it, resulted from modification and contraction of the axial viscera (see also Öpik 1967: 61). Why the position of the visceral termination in agnostoids should be indicated by a dorsal node does not seem to have been addressed by Öpik. Evidence from specimens of *Ptychagnostus affinis* (Robison 1984: 17) suggests that change in position of median nodes on the glabella does not necessarily represent migration, but in some specimens probably resulted from separate expression of different latent nodes. Consequently, I suggest that position of secondary nodes be used with caution in the taxonomy of agnostoids. Position of such nodes may be stable in some genera but variable in others. Moreover, the nodes are not necessarily homologous. In regard to *Ammagnostus*, I accord limited taxonomic significance to the position of secondary nodes.

Öpik (1967: 145) distinguished *Agnostoglossa* Öpik 1967, from *Ammagnostus* by its V-shaped rather than straight transglabellar furrow, differences in width of the cephalic border, minor differences in constriction of the cephalic acrolobe, and position of the secondary median node on the pygidium. In my opinion, these characters are of trivial importance, and I consider *Agnostoglossa* to be a junior synonym of *Ammagnostus*.

Glyptagnostus (Lispagnostus) Öpik 1967, is based on a single, poorly preserved cephalon. Its primary characters differ little from those of *Ammagnostus psammius* Öpik 1967, of similar age, and I consider *Lispagnostus* to be a synonym of *Ammagnostus*.

As emended, three species of *Ammagnostus* are identifiable. These are *A. psammius* (= *A. integriceps, A. euryaxis, Glyptagnostus (Lispagnostus) lenis,* all of Öpik 1967), *A. bassa* (Öpik 1967), and *A. beltensis* (Lochman in Lochman & Duncan 1944). *A. mitis* Öpik 1967, is based on two small pygidia that may represent *Ammagnostus,* but I consider their species assignment to be indeterminate.

Ammagnostus is known from Argentina, Australia, China, Greenland, the Soviet Union (Kazakhstan), and the United States. It has an observed stratigraphic range from the *Lejopyge laevigata* to the *Glyptagnostus stolidotus* zones.

Ammagnostus beltensis (Lochman in Lochman & Duncan 1944)

Figs 10.1–5, 19.12

Baltagnostus beltensis – Lochman in Lochman & Duncan 1944: 138–139, pl. 12: 3–5; Hu 1972: 254–258, pl. 30: 22–35

Baltagnostus sp. undet. – Wilson 1954: 284, pl. 24: 23

Baltagnostus wyomingensis – Lochman & Hu 1960: 822, pl. 99: 1–4

cf. *Baltagnostus wyomingensis* – Lochman & Hu 1960: 822, pl. 99: 32

Oedorhachis typicalis Resser – Robison 1960: 12–13, pl. 1: 7, 8

Baltagnostus hospitus – Poulsen 1960: 7–8, pl. 1: 5, 6

Baltagnostus mendozensis – Poulsen 1960: 8–9, pl. 1: 7

Homagnostus wyomingensis (Lochman & Hu) – Robison 1964: 531

Ammagnostus? beltensis (Lochman) – Öpik 1967: 113, 139

New material. – More than 30 cephala and pygidia in GGU 225529, 225546, 225547, and 271417.

Emended diagnosis. – Acrolobe unconstricted on cephalon, unconstricted to slightly constricted on pygidium. Pygidial axis weakly pyriform, secondary node terminal.

Remarks. – Palmer (1955: 718) concluded that the holotype pygidium of *Baltagnostus beltensis* "is certainly congeneric if not conspecific with *Kormagnostus simplex* Resser." Lochman & Hu (1960: 822) acknowledged that Palmer's statement "appears to be true," but defended the assignment of a paratype cephalon and pygidium to *Baltagnostus*. *B. wyomingensis* Lochman & Hu 1960, then was defined to include similar specimens from Wyoming. Öpik (1967: 139) subsequently suggested that *B. beltensis* "is probably an *Ammagnostus*." Further review has led me to the conclusion that the holotype pygidium of *B. beltensis* is congeneric with *Ammagnostus psammius* rather than *K. simplex* (= *K. seclusus* Walcott 1884) and I reassign *B. beltensis* to *Ammagnostus*.

Pygidia of *A. beltensis* and some *K. seclusus* are closely similar and may be difficult to distinguish. Generally, *A. beltensis* has a less constricted acrolobe, the border furrow is narrower, and the inner margin of the posterior border is more distinctly defined. Cephala of the two species can be easily distinguished by the lack of effacement of the anterior axial furrow in *A. beltensis*.

A. beltensis closely resembles *A. psammius* but it lacks strong constriction of the pygidial acrolobe. Also, the secondary node on the posteroaxis of *A. beltensis* is terminal rather than subcentral.

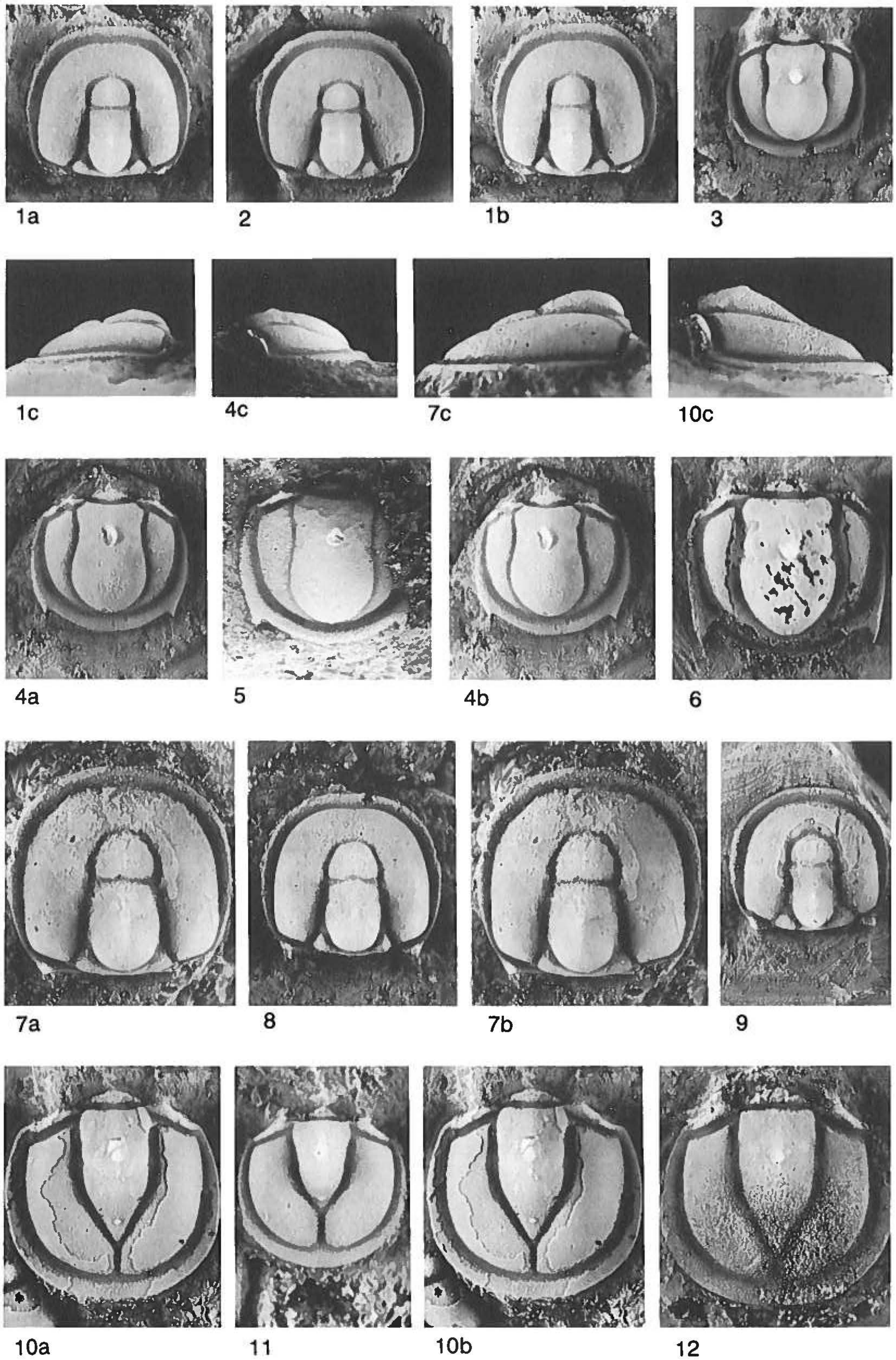
Occurrence. – *A. beltensis* is known from Argentina, Greenland, and the United States. Its observed stratigraphic range seems to be confined to the *Lejopyge laevigata* Zone. In Greenland, it is present in lime mudstone, packstone, and grainstone through the lower 111 m of the Holm Dal Formation.

Genus *Kormagnostus* Resser 1938

Kormagnostus – Resser 1938: 49; Lochman in Lochman & Duncan 1940: 24; Shimer & Shrock 1944: 600; Palmer 1954: 59; Palmer 1955: 718; Howell in Harrington et al. 1959: O185; Poulsen 1960: 11; Öpik 1967: 138–139

Type species. – *Kormagnostus simplex* Resser 1938, p. 49, pl. 9, figs 11–13 (= *Agnostus seclusus* Walcott 1884: 25, pl. 9: 14).

Emended diagnosis. – Cephalon subquadrate to subcircular. Axial furrow effaced around anteroglabella. Transglabellar furrow well defined, straight. Posteroglabella rounded at rear, median node near midpoint. Basal lobes simple. Genae smooth, anteriorly confluent. Pygidium subrectangular to ovoid, simplimarginate. Pygidial axis broad, parallel sided or expanding rearward, reaching posterior border furrow; ring furrows effaced; median tubercle small; terminal median node may be present. Acrolobe unconstricted on cephalon, constricted on pygidium. Cephalic and pygidial border furrows wide. Border of pygidium having pair of small posterolateral spines.


1a
2
1b
3
1c
4c
7c
10c
4a
5
4b
6
7a
8
7b
9
10a
11
10b
12

Remarks. – As emended, *Kormagnostus* includes a single, exceptionally variable species, *K. seclusus* (Walcott 1884). The cephalon of *Kormagnostus* closely resembles that of *Hypagnostus* Jaekel 1909, and *Tomagnostella* Kobayashi 1939a, but has a wider border furrow, especially in the late holaspid period. The pygidium of *Kormagnostus* can be rather easily distinguished from that of either *Hypagnostus* or *Tomagnostella* by its much more expanded axis.

An earlier suggestion (Robison 1964: 519) that *Homagnostus* is the ancestor of Kormagnostus was based on the generic assignment of a new species *Homagnostus incertus* Robison 1964, which subsequently has been reassigned to *Peronopsis* (see *Peronopsis incertus*, herein). Similarity in axial structure still indicates that *K. seclusus* may have been derived from *P. incertus* by effacement of the axial furrow around the anteroglabella. Lowest observed stratigraphic occurrences of the two species are in accord with such an inferred ancestry.

Kormagnostus is widespread in North America and here is described from North Greenland. It also is known from Argentina and the Soviet Union (Kazakhstan). Two poorly preserved specimens from Tasmania have been compared with *Kormagnostus* (Jago 1977: 48–49); however, their identity remains uncertain. Two reports of *Kormagnostus* in China (Yang 1978: 30–31, Liu 1982: 296) appear to be based on erroneous identifications. *Kormagnostus* has an observed stratigraphic range from at least the lower *Lejopyge laevigata* Zone to the *Glyptagnostus stolidotus* Zone. A previous report of *Kormagnostus* from the *Elvinia* Zone of Utah (Robison 1960: 10, 12) was erroneous.

Kormagnostus seclusus (Walcott 1884)

Fig. 11.5–15

Agnostus seclusus – Walcott 1884: 25, pl. 9: 14; Vogdes 1892: 395, pl. 10: 16
Kormagnostus simplex – Resser 1938: 49, pl. 9: 11–13; Shimer & Shrock 1944: pl. 251: 25–27; Rasetti 1946: 444–445, pl. 69: 32–34; Palmer 1955: 718–719, pl. 76: 8–12; Howell in Harrington et al. 1959: fig. 126, 2; Robison 1960: 12, pl. 1: 6, 11; Lochman & Hu 1960: 822–823, pl. 99: 5–31; Rasetti 1965: 38–39, pl. 1: 8, 9; Hu 1971: 72–74, pl. 7: 1–14; Hu 1985: 124–125; Hu 1986: 23, pl. 15: 16, 20–27, 29–31, 33–35; Ergaliev 1980: 75–76, pl. 4: 1–5
Kormagnostus harlanensis – Resser 1938: 49, pl. 10: 11, 12
Geragnostus (Geragnostella) seclusus (Walcott) – Kobayashi 1939a: 171–172
"Agnostus" nordicus – Lochman 1940: 23–24, pl. 2: 20–22
Kormagnostus esterius – Lochman 1940: 24–25, pl. 2: 32–35; Lochman in Lochman & Duncan 1944: 77, pl. 5: 15, 16; Lochman 1950: 348–349, pl. 51: 6–9
Kormagnostus senatus – Lochman 1940: 25, pl. 2: 36, 37
Kormagnostus splendens – Lochman 1940: 25–26, pl. 2: 23–31
Kormagnostus antiquus – Rasetti 1948: 321, pl. 45: 18–20
Kormagnostus seclusus (Walcott) – Palmer 1954: 59, pl. 13: 1–3
?*Kormagnostus cuchillensis* – Rusconi 1954: 48–49, text-fig. 25
Kormagnostus lanceolatus – Rusconi 1954: 49, text-fig. 26
Pseudagnostus? nordicus (Lochman) – Palmer 1955 (in part): 721, pl. 76: 7 (not 5); Robison 1960 (in part): 14, pl. 1: fig. 4 (not 1)
Baltagnostus hospitus – Poulsen 1960 (in part): 7–8, pl. 1: 6 (not 5)
Baltagnostus mendozensis – Poulsen 1960: 8–9, pl. 1: 7
Kormagnostus? propinquus – Poulsen 1960: 11–12, pl. 1: 10
?*Phoidagnostus solitariensis* (Rusconi) – Poulsen 1960: 14–15, pl. 1: 15
not *Kormagnostus antiquus* Rasetti – Yang 1978: 31, pl. 1: 25 (= *Proagnostus bulbus* Butts)

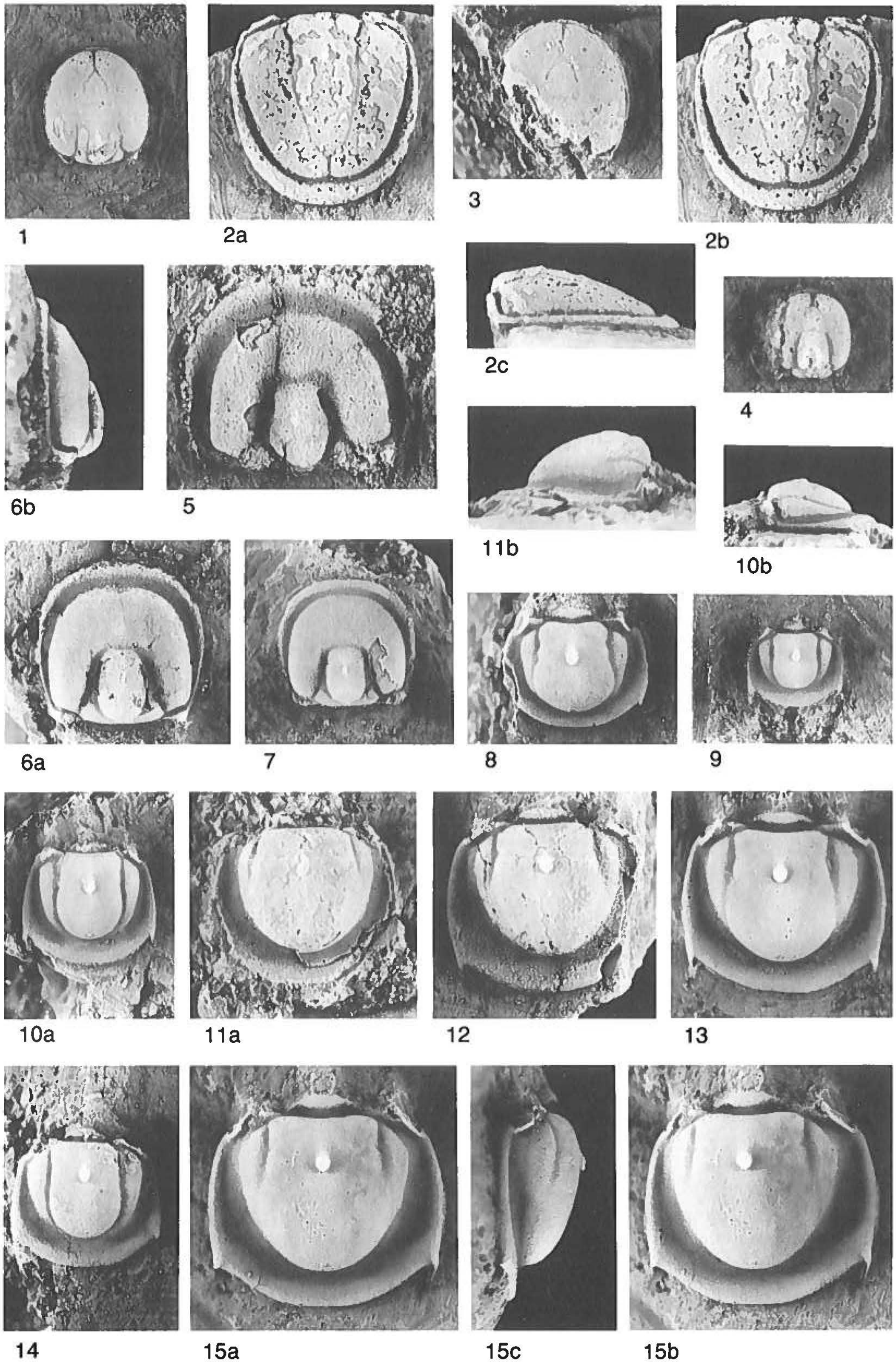
New material. – Numerous disarticulated sclerites in GGU 225528, 225529, 225535, 225537, 225539, 225540, 225547, 225552, 225561, 225563–225565, 271403, 271408, 271414, and 315013.

Diagnosis. – Characters of genus.

Remarks. – Large populations of *Kormagnostus* demonstrate exceptional variation in outline and convexity

Fig. 10. *Ammagnostus beltensis* (Lochman), *Peronopsis incertus* (Robison) and *Peronopsis tenuis* (Illing)

1–5. *Ammagnostus beltensis* (Lochman), all from GGU 271417, all X 8.8. 1. Cephalon in stereo (a, b) and left-lateral (c) views, MGUH 17.140. 2. Cephalon, MGUH 17.141. 3, 5. Intermediate and large holaspid pygidia, MGUH 17.142 and 17.143. 4. Pygidium in stereo (a, b) and left-lateral (c) views, MGUH 17.144.
6, 9. *Peronopsis incertus* (Robison), both from GGU 315012, both X 9.9. 6. Fragmentary pygidium, MGUH 17.145. 9. Intermediate holapsid cephalon, MGUH 17.146.
7, 8, 10–12. *Peronopsis tenuis* (Illing). 7. Large holaspid cephalon in stereo (a, b) and left-lateral (c) views, MGUH 17.147 from GGU 225529, X 8.8. 8. Intermediate holaspid cephalon, MGUH 17.148 from GGU 225563, X 8.8. 10. Partly exfoliated, large, holaspid pygidium showing the depressed back part of the posteroaxis and secondary median node; stereo (a, b) and left-lateral (c) views, MGUH 17.149 from GGU 271414, X 8.8. A small pyrite crystal protrudes through dorsal surface on anteroleft side of main median node. 11. Small holaspid pygidium with relatively short axis; MGUH 17.150 from GGU 225535, X 13.2. 12. Large, slightly corroded, holaspid pygidium, MGUH 17.151 from GGU 225529, X 7.7.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15a
15c
15b

of the pygidial axis. In dorsal view, the cephalon varies from subquadrate to subcircular. These and other variable features, some preservational, have been used to define several species that here are considered to be synonyms of *K. seclusus*. The new figured specimens have been selected to illustrate examples of this variation.

Considerable morphologic change also occurred during the ontogeny of *K. seclusus*. Some of this has been illustrated by Hu (1971, pl. 7:1–14; 1986, pl. 15:16, 20–27, 29–31, 33–35). Most of the pygidia that he identified as meraspides, however, do not retain at least one ankylosed thoracic segment and are therefore holaspides. Commonly small and intermediate holaspides have a parallel-sided pygidial axis, whereas in large holaspides the sides usually diverge rearward and the posterior axial furrow becomes effaced. On pygidia from several localities in North America and Greenland the axis expands rearward and becomes exceptionally tumid even in intermediate holaspides (e.g. Fig. 11.11, 12). Such tumid forms have previously been designated by the species name *nordicus*. In Argentina, *Phoidagnostus solitariensis* of Poulsen (1960) seems to be an example of the same form. During ontogeny the border furrows became relatively wider and this may be further accentuated by compression in fine-grained sediment.

Occurrence. – Same as genus. In North Greenland, *K. seclusus* ranges through the lower 111 m of the Holm Dal Formation and is present in all lithofacies.

Genus *Peronopsis* Hawle & Corda 1847

Type species. – *Battus integer* Beyrich 1845, p. 44, pl. 1, fig. 19.

Peronopsis incertus (Robison 1964)

Fig. 10.6, 9

Homagnostus incertus – Robison 1964: 531–532, pl. 82: 16, 17, 19, 20

Peronopsis incertus (Robison) – Öpik 1967: 139; Rushton 1978: 251

?*Peronopsis* sp. – Lin et al. 1983: 401, pl. 1: 2

New material. – Two cephala and one pygidium in GGU 315012.

Remarks. – Specimens from Greenland closely resemble somewhat older specimens from Utah that I previously described as *Homagnostus incertus*. Further analysis has led me to agree with Öpik (1967) that the species should be reassigned to *Peronopsis* (see also comment by Palmer 1968: B24).

P. incertus is characterized by a tumid, unfurrowed axis on the pygidium, which extends to the posterior border furrow. A pair of stout posterolateral spines on the pygidial border also is distinctive.

From a late Middle Cambrian drill core taken in Jiangsu Province, China, Lin et al. (1983) have figured a poorly preserved pygidium as *Peronopsis* sp. Its features appear to be identical to those of *P. incertus*, but assignment to that species remains questionable pending possible discovery of additional material, especially a cephalon. An associated pygidium was figured by Lin et al. as *Triplagnostus* sp., but it here is questionably reassigned to *Tomagnostella exsculpta* (Angelin 1851). The only collection from Greenland with *P. incertus* also contains *T. exsculpta*.

Occurrence. – *P. incertus* is known from Utah, Greenland, and possibly China. It has an observed stratigraphic range through most of the *Ptychagnostus punctuosus* and *Lejopyge laevigata* zones. In Greenland, rare specimens are preserved in dark lime mudstone from approximately 27 m above the base of the Holm Dal Formation of Freuchen Land.

Peronopsis tenuis (Illing 1916)

Fig. 10.7, 8, 10–12

Agnostus exaratus tenuis – Illing 1916: 406, pl. 28: 2–4; Nicholas 1916: 456

Fig. 11. *Lejopyge dubia* (Whitehouse) and *Kormagnostus seclusus* (Walcott).

1–4. *Lejopyge dubia* (Whitehouse). 1, 3. Intermediate, exfoliated(?), holaspid cephala; MGUH 17.152 and 17.153, both from GGU 315011, both X 8.8. 2. Large, mostly exfoliated pygidium in stereo (a, b) and left-lateral (c) views, MGUH 17.154 from GGU 315012, X 8.8. 4. Small holaspid(?) cephalon, MGUH 17.155 from GGU 315012, X 13.2.
5–15. *Kormagnostus seclusus* (Walcott). 5. Large cephalon compressed in lime mudstone, having well-rounded anterior and lateral margins, MGUH 17.156 from GGU 225540, X 8.8. 6, 7. Subquadrate, intermediate holaspid cephala; MGUH 17.157 and 17.158 from GGU 225561 and 271414, respectively, both X 8.8. 8. Intermediate holaspid pygidium showing more than usual rearward expansion of axis, MGUH 17.159 from GGU 225552, X 8.8. 9. Small holaspid pygidium, MGUH 17.160 from GGU 271414, X 13.2. 10, 14. Intermediate holaspid pygidia having common, parallel-sided axial form; MGUH 17.161 and 17.162 from GGU 225552 and 225561, respectively, both X 8.8. 11, 12. Tumid, moderately large pygidia having wide axis with exceptional rearward expansion and rearward effacement of axial furrow; MGUH 17.163 and 17.164, both from GGU 225561, both X 8.8. 13, 15. Moderately large and large pygidia (15 in stereo and right-lateral views) showing typical progressive effacement of posterior axial furrow with increase in size; MGUH 17.165 and 17.166, both from GGU 225547, both X 8.8.

Acadagnostus exaratus tenuis (Illing) – Kobayashi 1939a: 113
Peronopsis scutalis (Salter) – Westergård 1946 (in part): 41–42, pl. 4: 5–7, 10 (not 4, 8, 9, 11)
Agnostus sp. no. 6 – Westergård 1946: 98, pl. 16: 19
Baltagnostus hospitus – Poulsen 1960 (in part): 7–8, pl. 1: 5 (not 6)
Peronopsis ultima – Poulsen 1960: 13–14, pl. 1: 13
Peronopsis (Acadagnostus) scutalis (Salter in Hicks) – Hutchinson 1962 (in part): 72–73, pl. 6: 5 (not 1–4)
Peronopsis scutalis tenuis (Illing) – Rushton 1979: 50–51, fig. 3G

New material. – More than 50 cephala and pygidia in GGU 225529, 225535, 225537, 225563, 225565, 271414, ?315009, and ?315011.

Emended diagnosis. – *Peronopsis* lacking spines. Cephalon subcircular to subquadrate; axis robust, slightly tapered; median node very weak, near midlength of posteroglabella. Pygidium subcircular. Ring furrows effaced. Posteroaxis reduced in size and length, strongly tapered; separation from border furrow decreased during ontogeny; rear half depressed, terminating in acute point. Median tubercle of pygidium small, probably near back margin of effaced second ring; secondary median node may be present on depressed posteroaxis, slightly forward from tip.

Remarks. – Specimens from Greenland, here assigned to *P. tenuis*, are among the youngest reported representatives of a lineage seemingly derived from *P. acadicus* (Dawson 1868). Based on comparison of type material, I consider the commonly cited *P. scutalis* (Salter in Hicks 1872) to be a subjective junior synonym of *P. acadicus*. *P. tenuis* has a shorter, narrower, and more sharply pointed posteroaxis than *P. acadicus*. Forms of both taxa appear as low as the *Ptychagnostus gibbus* Zone. Morphological intermediates are common into the lower *Ptychagnostus punctuosus* Zone and their assignment to species may be arbitrary. During the phylogeny of *P. tenuis*, the back part of the posteroaxis became more depressed and specimens in the *Lejopyge laevigata* Zone commonly have a secondary median node slightly forward from the acute terminal tip.

Occurrence. – As revised, *P. tenuis* is known from Argentina, Canada (eastern Newfoundland), Greenland, Great Britain, and Scandinavia. It has an observed stratigraphic range from the *P. gibbus* to the *L. laevigata* zones, which is an unusually long range for a Middle Cambrian agnostoid species. In the lower 27 m of Holm Dal Formation it is common in lime packstone and grainstone, and rare in wackestone and mudstone.

Family Ptychagnostidae Kobayashi 1939a

Remarks. – Although *Tomagnostella* is reassigned here to the Ptychagnostidae, this action requires no emendation of the family diagnosis given by Robison (1984).

Genus *Lejopyge* Hawle & Corda 1847

Type species. – *Battus laevigatus* Dalman 1828, pp. 136–137.

Remarks. – The generic concept of Robison (1984: 36–37) is followed here. Contrary to many previous citations (including Robison 1984), the correct authorship of the generic name is Hawle & Corda 1847, rather than Corda (see discussion by Horny & Bastl 1970: 28–29, 40–43).

Lejopyge armata (Linnarsson 1869)

Fig. 12.1

Agnostus laevigatus var. *armata* – Linnarsson 1869: 82, pl. 2: 58, 59
Lejopyge laevigata armata (Linnarsson) – Liu 1982: 292, pl. 209: 7; Qiu et al. 1983: 38, pl. 13: 2
Lejopyge zhejiangensis – Qiu in Qiu et al. 1983: 38, pl. 18: 3
Lejopyge armata (Linnarsson) – Lermontova 1940: 130, pl. 36: 11a-c; Lu & Lin 1983: pl. 1: 7, 8; Bruton et al. 1984: 321–322, fig. 4H-M; Robison 1984: 39–40, fig. 22 (see for additional synonymy)

Material. – Six cephala and one pygidium in GGU 225544, 225546, and 271414.

Remarks. – The taxonomy and distribution of *L. armata* was recently reviewed by Robison (1984: 39–40), including the analysis of available material from North Greenland. *L. armata* is the only species of *Lejopyge* to possess border spines on both the cephalon and pygidium.

Occurrence. – In North Greenland, *L. armata* is rare in dark lime mudstone and wackestone from 12 to 110 m above the base of the Holm Dal Formation.

Lejopyge dubia (Whitehouse 1936)

Fig. 11.1–4

Phalacroma(?) dubium – Whitehouse 1936: 95–96, pl. 9: 13–15

Pseudophalacroma crebra – Pokrovskaya 1958: 79–80, pl. 3: 4–6; Egorova, Pegel, & Chernysheva in Egorova et al. 1982: 76, pl. 12: 12, pl. 27: 17, pl. 42: 1, 2, 5, pl. 46: 3, pl. 47: 4
Pseudophalacroma crebrum Pokrovskaya – Öpik 1961: 90–91
Pseudophalacroma dubium (Whitehouse) – Öpik 1961: 93–94, pl. 22: 5–10; Öpik 1979: 163–164, pl. 67: 1–4; Ergaliev 1980: 80–81, pl. 2: 4–7; Xiang & Zhang 1985: 78, pl. 14: 13–19
Pseudophalacroma aff. *dubium* (Whitehouse) – Chu 1965: 139, pl. 1: 24, 25
Leiopyge praecox – Öpik 1979: 159–160, pl. 41: 1. pl. 66: 1–7
Leiopyge cosfordae – Öpik 1979: 160–161, pl. 65: 1, 2
?*Pseudophalacroma breviovata* – Ju in Qiu et al. 1983: 38–39, pl. 13: 5, 6
Lejopyge dubium (Whitehouse) – Robison 1984: 37
?*Phalacroma* sp. – Xiang & Zhang 1985: 78, pl. 14: 20

New material. – Three cephala and one pygidium in GGU 315011 and 315012.

Emended diagnosis. – *Lejopyge* having wide pygidial border; width increasing posteriorly, relative posterior width increasing during ontogeny. Dorsal furrows on acrolobes becoming mostly effaced by early holapid period; vestiges may be evident on exfoliated holapides. Cephalic border very narrow. Pygidial acrolobe becoming constricted during holaspid ontogeny. Spines lacking.

Remarks. – As emended here, *L. dubia* is characterized by a very narrow cephalic border, simple basal lobes, an especially wide pygidial border and a lack of spines. Although late holaspides show advanced effacement of furrows on the acrolobes, early holaspides may show a weak pattern of ptychagnostid furrows. Exfoliated holaspides are variable in showing vestiges of these furrows, seemingly influenced by conditions of preservation. Specimens in limestone may show vestiges of furrows of the acrolobes, whereas those in shale or sandstone usually show none, except near the thorax.

Where evident, the axial structure of *L. dubia* closely resembles that of *L. lundgreni* (Tullberg 1880), its inferred ancestor. *L. dubia* differs from *L. lundgreni* by its advanced effacement of dorsal furrows and its wider border on late holaspides. Vestigial features also indicate a narrower, more lanceolate posteroaxis on the pygidium of large holaspides, which seems to be a paedomorphic condition (cf. Fig. 11.2 with Robison 1984: fig. 27: 4, 8).

From review of available information, I consider *Pseudophalacroma crebra* Pokrovskaya 1958, *Leiopyge praecox* Öpik 1979, and *L. cosfordae* Öpik 1979, to be subjective junior synonyms of *L. dubia*. Characters that have been used to differentiate these species are here attributed either to individual variation, ontogenetic change, or taphonomic alteration.

Morphologically, and probably phylogenetically, *L. dubia* is intermediate between *L. lundgreni* and *L. multifora* Öpik 1979. Derived characters of the latter species include paired spines on the cephalon and the posterior thoracic segment as well as conspicuous punctation of the test.

Pseudophalacroma (= Lejopyge) triangularis Ju in Qiu et al. (1983: 38, pl. 13: 4; see also Lu & Lin 1983, pl. 1: 5, 6) closely resembles *L. dubia* in degree of furrow effacement and in structure of cephalic and pygidial borders, but both the cephalon and pygidium have a distinctive triangular outline. Based on comparison of undescribed specimens of *L. triangularis* from the Huaqiao Formation of western Hunan and the few specimens of *L. dubia* from North Greenland, the differences in tagmatic outline are maintained throughout holaspid ontogeny.

Occurrence. – As emended, *L. dubia* is known from Australia, China, the Soviet Union, and Greenland. It has an observed stratigraphic range from the *Ptychagnostus punctuosus* Zone through most of the *Lejopyge laevigata* Zone. In North Greenland it is rare in dark lime mudstone from about 27 m above the base of the Holm Dal Formation of Freuchen Land.

Lejopyge laevigata (Dalman 1828)

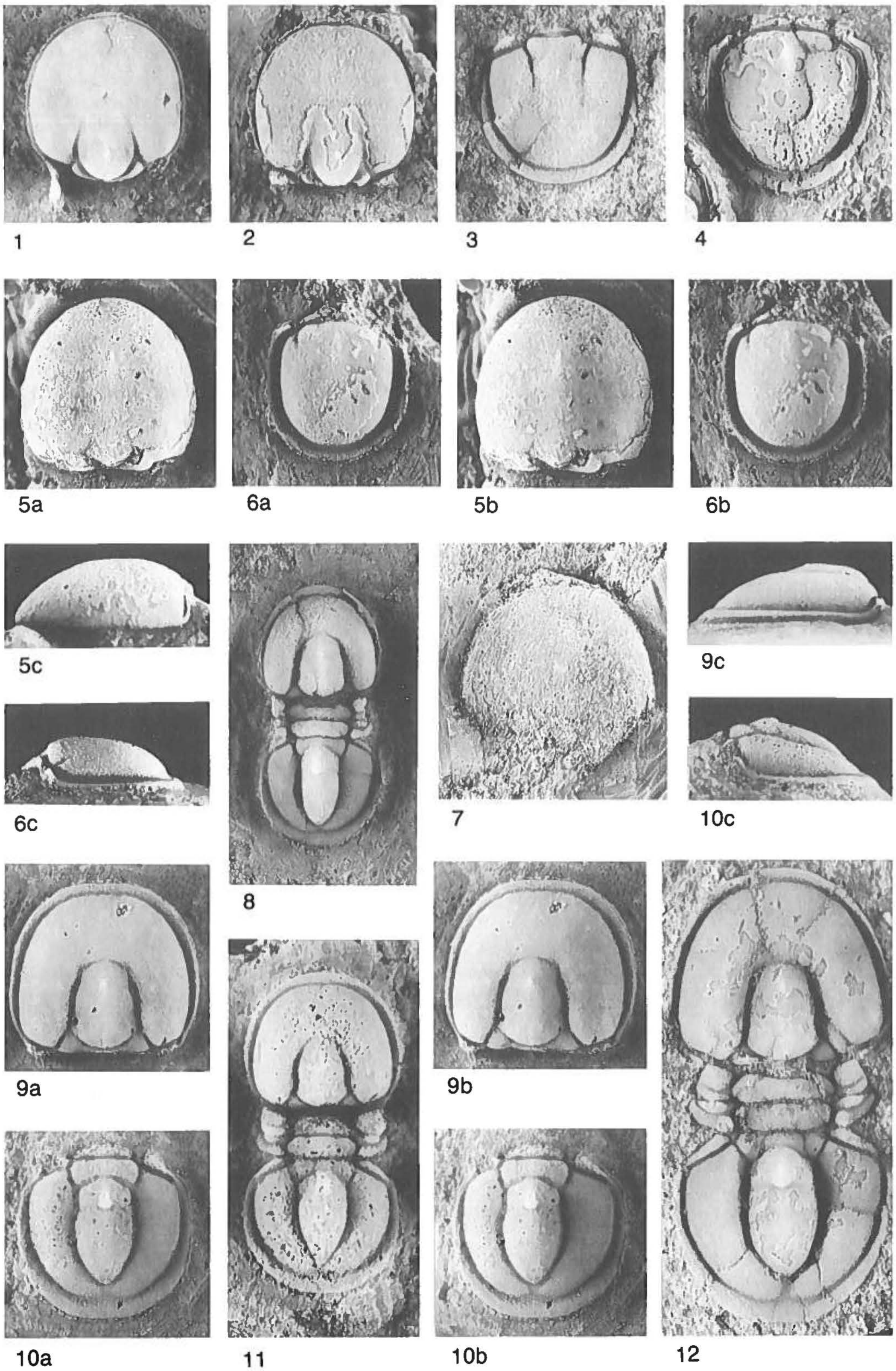
Fig. 12.2, 3

Battus laevigatus – Dalman 1828: 136–137
Lejopyge laevigata (Dalman) – Hawle & Corda 1847: 51, pl. 3: 25; Robison 1984: 42–46 (see for additional synonymy); Whittington 1986: 174–175, pl. 19: 1–3, pl. 20: 1

Material. – At least 8 cephala and 10 pygidia in GGU 225535, 225537, 225543, 225544, 225546, 225552, 225561, and 225595.

Remarks. – The taxonomy and distribution of *L. laevigata* was recently reviewed by Robison (1984: 44–46), including an analysis of available material from North Greenland. *L. laevigata* is nonspinose and the pygidial border is of moderate width. Furrows of the acrolobes are mostly effaced except for the basal furrows and distally shallowing axial furrows along most of the posteroglabella and the anteroaxis.

Occurrence. – In North Greenland, *L. laevigata* is rare in lime mudstone and grainstone, ranging through most of the Holm Dal Formation.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5c
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9c
6c
10c
9a
9b
12
10a
11
10b

Genus *Tomagnostella* Kobayashi 1939a

Tomagnostella – Kobayashi 1939a: 150–151; Howell in Harrington et al. 1959: O186; Öpik 1979: 71–72

Type species. – *Agnostus exsculptus* Angelin 1851, p. 7.

Emended diagnosis. – Cephalon having axial furrow effaced around anteroglabella. Preglabellar median furrow usually effaced, rarely incomplete. Posteroglabella rounded at rear. Basal lobes simple. Pygidial axis widest at M1, weakly constricted at M2; F2 shallower than F1. Posteroaxis lanceolate, receding from border furrow during ontogeny. Postaxial median furrow usually present following separation of axis from border furrow.

Remarks. – Several authors (e.g. Westergård 1946, Pokrovskaya in Chernysheva 1960) have considered *Tomagnostella* to be a junior synonym of *Hypagnostus* Jaekel 1909. Others (Howell in Harrington et al. 1959, Öpik 1979) have recognized *Tomagnostella* as a valid genus. Although I previously considered *Tomagnostella* to be a synonym of *Hypagnostus* (Robison 1964), discussion by Öpik (1979) and further evaluation have convinced me that *Tomagnostella* should be accepted as a valid genus.

The origin of *Tomagnostella* seems to be within the Ptychagnostidae. *Lejopyge lundgreni* (sensu Robison 1984) and *Tomagnostella exsculpta* are closely similar, especially in axial structure, and I suggest that either they share a close common ancestor or *T. exsculpta* was derived from an early branch of *L. lundgreni* by effacement of at least part of the preglabellar median furrow and an anterior part of the axial furrow. In this regard, it seems significant that the anteroglabella of *L. lundgreni* is low in profile, being flush with or little elevated above the genae (Robison 1984: 46).

Tomagnostella is a close homeomorph of *Hypagnostus*, the ancestral species of each probably being derived from different species (*Hypagnostus* from a species of *Peronopsis*) by effacement of the anterior axial furrow. Similar effacement was repeated in other lineages of Cambrian agnostoids, giving rise to such other homeomorphic genera as *Eoagnostus* Resser & Howell 1938, and *Kormagnostus*.

Tomagnostella and *Hypagnostus* can be most easily distinguished by features of the pygidial axis. In *Tomagnostella* the axis is distinctly narrower behind the first ring (M1) and its posterior end is more pointed. In *Hypagnostus* the two ring furrows are usually effaced, but in *Tomagnostella* at least the first furrow (F1) is always developed.

Based on available information, species here included in *Tomagnostella* are *T. exsculpta*, *T. denticulata* (Westergård, 1946), and *T. hippala* (Öpik 1961). Other named taxa may warrant reassignment when features become better known.

As emended, representatives of *Tomagnostella* have been described from Australia, China, England, Scandinavia, and the Soviet Union. New specimens are described here from Greenland and I have collected many undescribed specimens from the western United States. Based on glabellar shape, a single cephalon from Alaska, which Palmer (1968: B31, pl. 6: 26) figured as *Hypagnostus* sp., may represent *Tomagnostella*. Except for questionable occurrences, the genus is restricted to the *Ptychagnostus punctuosus* and *Lejopyge laevigata* zones of Robison (1984).

Tomagnostella exsculpta (Angelin 1851)

Fig. 12.8–12

Agnostus exsculptus – Angelin 1851 (in part): 7, pl. 6: 8 (cephalon only); Tullberg 1880: 22, pl. 1:10; Wallerius 1895: 37, pl. 1: 1; 1930: 58, fig. 5a, c; Grönwall 1902: 53–54

Agnostus parvifrons nepos – Brøgger 1878: 72, pl. 6: 2

Agnostus parvifrons Linnarsson – Tullberg 1880 (in part): 34–35, pl. 2: 28 (forma 3 only)

Agnostus exsculptus sulcifera – Wallerius 1895: 38, pl. 1: 1

Agnostus exsculptus integra – Wallerius 1895: 38

Ptychagnostus exsculptus (Angelin) – Jaekel 1909: 400

not *Agnostus parvifrons nepos* Brøgger – Strand 1929: 348, pl. 1: 16 [= *Hypagnostus parvifrons* (Linnarsson 1869)]

Fig. 12. *Lejopyge armata* (Linnarsson), *Lejopyge laevigata* (Dalman), *Toragnostus bituberculatus* (Angelin), *Grandagnostus vermontensis* Howell and *Tomagnostella exsculpta* (Angelin).

1. *Lejopyge armata* (Linnarsson), cephalon, MGUH 16.278 from GGU 225544, X 8.8.
2, 3. *Lejopyge laevigata* (Dalman), mostly exfoliated cephalon and latex cast of testaceous pygidium, MGUH 17.167 and 17.168 from GGU 225561 and 225543, respectively, both X 8.8.
4–6. *Toragnostus bituberculatus* (Angelin), n. gen. 4. Pygidium compressed in lime mudstone, MGUH 17.169 from GGU 225586, X 7.7. 5. Mostly exfoliated cephalon in stereo (a, b) and left-lateral (c) views, MGUH 17.170 from GGU 271414, X 7.7. 6. Exfoliated pygidium in stereo (a, b) and left-lateral (c) views, MGUH 17.171 from GGU 271414, X 8.8.
7. *Grandagnostus vermontensis* Howell, holotype, incomplete cephalon(?) compressed in dark-grey slate, St. Albans Shale from near St. Albans, Vermont; Princeton University no. 9736, X 3.3.
8–12. *Tomagnostella exsculpta* (Angelin), all X 8.8. 8, 11, 12. Complete dorsal exoskeletons, each with subcircular cephalon, and showing progressive decrease in relative length of pygigial axis with increase in holaspid size; MGUH 17.172–17.174 from GGU 225586, 271408, and 225586, respectively. 9. Subquadrate cephalon in stereo (a, b) and left-lateral (c) views, MGUH 17.175 from GGU 271408. 10. Pygidium in stereo (a, b) and left-lateral (c) views, MGUH 17.176 from GGU 271408.

Agnostus exsculptus didymus – Wallerius 1930: 58, fig. 5b
Hypagnostus exsculptus (Angelin) – Whitehouse 1936: 104; Whitehouse 1939: 263; Westergård 1946: 50–51, pl. 5: 35, pl. 6: 1, 2, ?3–5; Pokrovskaya 1958: 84–86, pl. 3: 10–12; Khairullina 1970: 15, pl. 1: 3; Khairullina 1973: 41–42, pl. 3: 5–7; Romanenko 1977: 166, pl. 23: 15, 16; Egorova, Pegel & Chernysheva in Egorova et al. 1982: 72, pl. 42: 6, pl. 46: 4
Hypagnostus parvifrons nepos (Brøgger) – Kobayashi 1939a: 123
Tomagnostella exsculpta (Angelin) – Kobayashi 1939a: 150–151; Howell in Harrington et al. 1959: fig. 127:2; Öpik 1979: 72
Tomagnostella exsculpta sulcifera (Wallerius) – Kobayashi 1939a: 150–151
Tomagnostella exsculpta integra (Wallerius) – Kobayashi 1939a: 150–151
Hypagnostus nepos (Brøgger) – Westergård 1946: 47–48, pl. 5: 5–8; Yang 1978: 27, pl. 2: 14, 15; Yang 1982: pl. 2: 8, 9; Egorova, Pegel, & Chernysheva in Egorova et al. 1982: 70, pl. 23: 1, 2, 13, pl. 27: fig. 16, pl. 41: 1, 2
?*Hypagnostus exsculptus geminus* – Westergård 1946: 52, pl. 6: 6
Hypagnostus sulcifer (Wallerius) – Westergård 1946 (in part): 52, pl. 6: 7–10, 12–17 (not 11); Rushton in Taylor & Rushton 1972: 9, pl. 4; Romanenko 1977: 166, pl. 23: 13, 14; Rushton 1978: 254, pl. 24: 3, 4; Ergaliev 1980: pl. 4: 7, 8; Egorova, Pegel, & Chernysheva in Egorova et al. 1982: 70, pl. 26: 1; Yang 1982: pl. 2: 2
Hypagnostus sulcifer integer (Wallerius) – Westergård 1946: 52, pl. 6: 18, 19
Hypagnostus hunanicus – Lu 1957: 258, pl. 137: 8–10; Wang Yu et al. in Wang Yu 1964: 29, pl. 3: 7, 8, pl. 4: 8; Lu et al. 1965: 45, pl. 5: 1–3; Zhou et al. 1977: 115, pl. 37: 19–21; Yin 1978: 389, pl. 144: 8, 9; Liu 1982: 295, pl. 210: 6, 7, 10, pl. 11: 1
Hypagnostus quadratus – Lu 1957: 258, pl. 137: 11–13; Egorova et al. 1963: 66–67, pl. 7: 11, 12; Wang Yu et al. in Wang Yu 1964: 29, pl. 5: 3, 4; Wang Shuei et al. in Wang Yu 1965: 30, pl. 3: 13, 14, pl. 6: 12; Lu et al. 1965: 46, pl. 5: 7–9; Chu 1965: 137, pl. 1: 13; Yin 1978: 390, pl. 144: 15, 16; Xiang 1981: pl. 7: 8
Hypagnostus cf. *exsculptus* (Angelin) – Yang 1978: 26–27, pl. 2: 10
Tomagnostella nepos (Brøgger) – Öpik 1979: 72–73, pl. 67: 5
Tomagnostella sulcifer (Wallerius) – Öpik 1979: 72
Tomagnostella sulcifer integer (Wallerius) – Öpik 1979: 72
?*Hypagnostus stigmaeus* – Liu 1982: 295, pl. 211: 9, 10, 12
?*Hypagnostus angulus* – Liu 1982: 295–296, pl. 211: 2, 11
?*Triplagnostus* sp. – Lin et al. 1983: 401, pl. 1: 3

New material. – Numerous specimens in GGU 225528, 225529, 225535, 225552, 225561, 225564, 225586, 225595, 271408, 271414, 271417, 315007, 315009, and 315011–315013.

Emended diagnosis. – Cephalon subcircular to subquadrate. Posteroglabella approximately half length of cephalon; front commonly angular, sides commonly with slight outward bow near middle; median node anterior from midpoint. Genae smooth to moderately scrobiculate. Front part of preglabellar median furrow may be weakly incised, generally in specimens also having scrobicules. Second ring furrow of pygidium shallower than first. Second axial ring having small median tubercle near posterior margin.

Remarks. – As emended, *T. exsculpta* is variable with regard to dorsal outline of the cephalon, depth of ring furrows on the pygidium, and presence both of genal scrobicules and an incomplete preglabellar median furrow. Also, relative length of the pygidial axis decreased during holaspid ontogeny. One or more of these characters has been cited in definitions of several otherwise similar taxa (see synonymy). Because these features are variable either in populations of *Tomagnostella* from Greenland or in related ptychagnostid species, I do not accord them significant taxonomic value. Other named taxa (e.g. *Hypagnostus willsi* Öpik 1961, *H. durus* Öpik 1967) may prove to be synonyms of *T. exsculpta* when better preserved specimens become available.

Occurrence. – *T. exsculpta* is known from Australia, China, England, Greenland, Scandinavia, the United States (undescribed specimens, Nevada and Utah), and the Soviet Union. It has an observed stratigraphic range from the *Ptychagnostus punctuosus* Zone through most of the *Lejopyge laevigata* Zone. In Greenland, specimens are present in most lithofacies of the Holm Dal Formation, but they are most common in dark lime mudstone. The species ranges through most of the formation.

Family uncertain

Genus *Toragnostus* n. gen.

Type species. – *Agnostus bituberculatus* Angelin 1851, p. 6, pl. 6, fig. 2.

Diagnosis. – Agnostoids having advanced effacement of axial furrows. Cephalon retaining basal lobes and posterior border furrows but lacking lateral and anterior border furrow. Median glabellar node weak, elongate, and well anterior from cephalic midpoint. Pygidium less convex than cephalon; axis exceptionally wide as indicated by anterior vestiges of axial furrow; median node weak, elongate, and near front of pygidium; border moderately wide.

Remarks. – *Agnostus bituberculatus* Angelin has been reassigned to either *Phoidagnostus* Whitehouse 1936, or *Phalagnostus* Howell 1955, by various authors. From review of the type specimens of *Phoidagnostus limbatus* Whitehouse 1936, the type species of *Phoidagnostus,* Öpik (1961: 86) concluded that they probably are compressed representatives of either *Lejopyge armata* or *L. laevigata.* Hence, *Phoidagnostus* has been suppressed as a subjective junior synonym of *Lejopyge* (Öpik 1967: 76; Robison 1984: 36–37). As indicated by vestiges of furrows in the perithoracic region, *A. bituberculatus* has a much wider axis than does any species of *Lejopyge,* and advanced effacement of furrows in the two morphic groups appears to be the result of convergence rather than synapomorphy. *Battus nudus* Beyrich 1845, the type species of *Phalagnostus,* is characterized by transverse furrows at the anterolateral corners of the pygidium and seems to lack a lateral and posterior border on the pygidium (Rasetti 1967: 38–39; Jago 1976: 144–146). Because *A. bituberculatus* has a normal pygidial border, it should not be assigned to *Phalagnostus,* and as noted by Öpik (1967: 76) no generic name is available for the species. To remedy that problem, the new genus *Toragnostus* here is erected to receive *A. bituberculatus.*

Rushton (1978: 255) reassigned *A. bituberculatus* Angelin to *Grandagnostus* Howell 1935a. The holotype of *G. vermontensis* Howell 1935a, the type species of *Grandagnostus,* is a poorly preserved, incomplete, smooth, probable cephalon, which is illustrated here (Fig. 12.7) for comparison. Because that holotype lacks definitive taxonomic characters, I propose that application of the name *Grandagnostus* be restricted to it.

In addition to *G. vermontensis,* Rushton (1978) also considered *Agnostus cicer* Tullberg 1880, *Ciceragnostus? falanensis* Westergård 1947, *Phoidagnostus angustiformis* Pokrovskaya 1958, *Phalacroma maja* Pokrovskaya 1958 (?part), *Grandagnostus velaevis* Öpik 1961, *Phalacroma bairdi* Hutchinson 1962, and *Grandagnostus* sp. of Jago 1976, to be related generically to *A. bituberculatus.* All of these taxa include effaced agnostoids having a border on the pygidium but none on the cephalon. Of the taxa listed, only *bituberculatus* has been demonstrated to have an elongate median node situated well anterior from the cephalic midpoint. Among agnostoids, such a far anterior node is exceptional and suggests some modification of internal anatomy. Therefore, I attach more taxonomic importance to that nodal position than to reduction or effacement of the cephalic border. Based on available information, *A. bituberculatus* is the only species reassigned to *Toragnostus* at this time.

Toragnostus bituberculatus (Angelin 1851)

Fig. 12.4–6

Agnostus bituberculatus – Angelin 1851: 6, pl. 6: 2; Westergård in Holm & Westergård 1930: 11–12, pl. 1: 10–12, pl. 4: 4–6

not *Agnostus bituberculatus* (Angelin) – Brøgger 1878: p. 75, pl. 6: 9 [= *Cotalagnostus confusus* (Westergård in Holm & Westergård 1930)]

Agnostus glandiformis (Angelin) – Grönwall 1902 (in part): 63–64, pl. 1: 6 (not 7)

Phoidagnostus bituberculatus (Angelin) – Whitehouse 1936: 93; Kobayashi 1939a: 136; Lermontova 1940: 130, pl. 36: 6, 6a-d; Westergård 1946: 91–92, pl. 14: 10–14; Ivshin 1953: 25–27, pl. 1: 1–9; Pokrovskaya 1958: 39, pl. 3: 13, 14; Pokrovskaya in Chernysheva 1960: pl. 1: 24, 25; Rosova 1964: 19, pl. 3: 13–20; Repina et al. 1975: 119, pl. 11: 15–19; ?Romanenko 1977: 168, pl. 23: 23, 24; ?Egorova et al. 1982: 76, pl. 15: 5

Phalagnostus bituberculatus (Angelin) – Öpik 1961: 54; Palmer 1968: B32, pl. 6: 13

Grandagnostus bituberculatus (Angelin) – Rushton 1978: 255

New material. – Two cephala and two pygidia in GGU 225586 and 271414.

Remarks. – Specimens from North Greenland agree well with Westergård's (1946) description and illustrations of material from the type area of Sweden. The new pygidia are relatively small and have a border of fairly uniform width, as do smaller Swedish holaspides, whereas the border of larger Swedish holaspides are slightly widened at the sides. The smallest new pygidium also has short vestiges of anterior axial furrows; however, the specimen is exfoliated, and such furrows have not been observed on larger testaceous specimens.

Occurrence. – *T. bituberculatus* has been previously reported from Sweden, Denmark, the Soviet Union (Bennett Island, Kazakhstan, Siberia, Turkestan), and the United States (Alaska). I have collected undescribed specimens from the upper Huaquiao Formation of western Hunan Province, China. In North Greenland *T. bituberculatus* is rare in dark lime wackestone and mudstone from about 12 and 25 m, respectively, above the base of the Holm Dal Formation. The species appears to be restricted to the *Lejopyge laevigata* Zone of Robison (1984).

Order Polymerida
Family Asaphiscidae Raymond

Genus *Blountia* Walcott 1916b

Type species. – *Blountia mimula* Walcott 1916b, pp. 399–400, pl. 61, figs 4, 4a-c.

Remarks. – The generic concept of Palmer (1962: F-22) is followed here.

Blountia bella n. sp.

Fig. 13.5, 8–12

Holotype. – Pygidium (Fig. 13.11a, b), MGUH 17.185 from GGU 271417.

Material. – More than 25 cranidia and pygidia in GGU 271417.

Diagnosis. – Cranidium highly vaulted with exceptionally long, slightly tapered axis. Pygidium longer than usual, moderately convex, with well-developed anterior pair of pleural furrows. Pygidial axis relatively wide at posterior end. Pygidial border doubles in width from front to back.

Description. – Cranidium highly vaulted, broadly rounded anteriorly. Axis proportionately large and elongate, slightly tapering forward. Occipital furrow effaced. Frontal area short, length about 0.15 times that of cranidium; border furrow narrow but distinct, broadly curved forward; preglabellar field moderately downsloping; anterior border nearly horizontal, slightly convex, subequal in sagittal length to preglabellar field. Palpebral area of fixigena narrow, moderately downsloping. Eye ridge and palpebral lobe poorly defined. Posterior fixigena about half as wide as posterior axis in vertical dorsal view. Anterior sections of facial suture slightly divergent, straight; posterior sections divergent, slightly sinuous.

Pygidium moderately convex, subparabolic in outline; length relative to width increasing from about 0.7 to 0.9 during holaspid ontogeny. Axis weakly defined, lateral sides slightly concave; posterior end relatively wide, bluntly rounded, slightly indenting border furrow. Ring furrows nearly effaced but vestiges indicate at least eight axial rings. Pleural field nearly smooth except for deep, wide, and slightly oblique pleural furrow extending from anterior axis to lateral pygidial margin. Anterolateral articulating facet flat and prominent. Border furrow shallow but distinct, terminating against anterior pair of pleural furrows. Border nearly doubles in width progressing posteriorly.

Remarks. – In maximum size, *B. bella* is a relatively large species of *Blountia*. It differs from other species of the genus by its long cranidial axis and elongate pygidium with relatively wide posterior axis. Although the pygidial border furrow is shallow, it is better developed than in most species of the genus.

In size and shape of cranidial axis, *B. bella* appears to be most similar to *B. kindlei* Resser 1942, but has a shorter frontal area and narrower fixigenae. Also, axial and border furrows on the pygidium are much better developed.

Occurrence. – *B. bella* is common in a dolomitized trilobite packstone from about 92 m above the base of the Holm Dal Formation.

Blountia sp. 1

Fig. 13.7

Remarks. – Two pygidia in GGU 225552 are similar to *B. bella* in dorsal outline, but differ in lacking a distinct border furrow. Evidence of segmentation also is more effaced, the posterior end of the axis is narrower, and in side view the posterior slope is much steeper. These specimens do not appear to represent any described species of *Blountia*. They are preserved in lime grainstone from near the base of the Holm Dal Formation.

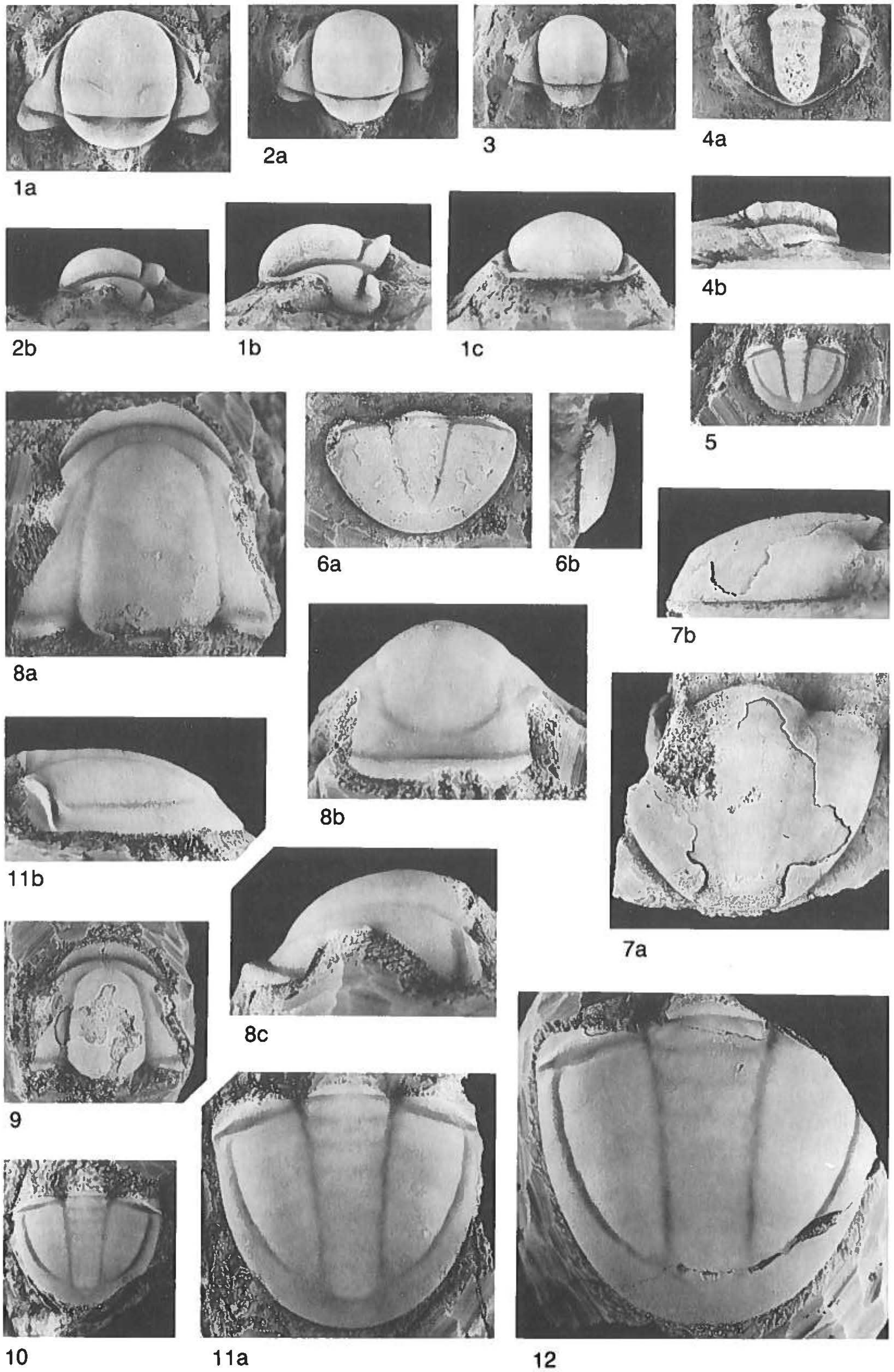
Blountia sp. 2

Fig. 13.6

Remarks. – A single, partly exfoliated, semicircular pygidium in GGU 225561 differs from that of *B. bella* in being proportionately shorter, having a more evenly tapered axis, and its border furrow is much less distinct. It resembles *Blountia* sp. 1 in effacement of furrows, but is proportionately shorter and the anterior axis is narrower than adjacent pleural regions. It somewhat resembles the pygidium of *B. arcuosa* Resser 1938 (cf. Rasetti 1965, pl. 9: 5–8), but the axial segmentation is much less evident on the internal mold. The specimen does not appear to represent any described species of

Fig. 13. *Catillicephala rotunda* (Rasetti), *Blountia bella* n. sp., *Blountia* sp. 1 and *Blountia* sp. 2.

1–4. *Catillicephala rotunda* (Rasetti), all from GGU 225552. 1–3. Holaspid cranidia of decreasing ontogenetic size; MGUH 17.177–17.179; X 4.4, 5.5, 6.6, respectively. 4. Exfoliated pygidium, MGUH 17.180, X 5.5.
5, 8–12. *Blountia bella* n. sp., all from GGU 271417, all X 3.3. 5, 10. Smaller pygidia, MGUH 17.181 and 17.182. 8, 9. Larger and smaller cranidia, MGUH 17.183 and 17.184. 11. Holotype pygidium in dorsal (a) and left-lateral (b) views, MGUH 17.185. 12. Exceptionally large, incomplete pygidium, MGUH 17.186.
6. *Blountia* sp. 2, pygidium in dorsal (a) and left-lateral (b) views, MGUH 17.187 from GGU 225561, X 3.3.
7. *Blountia* sp. 1, partly exfoliated pygidium in dorsal (a) and right-lateral (b) views, MGUH 17.188 from GGU 225552, X 3.3.


1a
2a
3
4a
2b
1b
1c
4b
5
6a
6b
7b
8a
8b
11b
7a
8c
9
10
11a
12

Blountia. It is preserved in lime grainstone from near the base of the Holm Dal Formation.

Family Catillicephalidae Raymond

Genus *Catillicephala* Raymond 1938

Type species. – *Cephalocoelia ovoides* Raymond 1937, p. 1124, pl. 3, fig. 22.

Remarks. – The family and generic concepts of Rasetti (1954) are followed here.

Catillicephala rotunda (Rasetti 1946)

Fig. 13.1–4

Cephalocoelia rotunda – Rasetti 1946: 450, pl. 68: 18–23
Catillicephala lata (Raymond) – Shaw 1952 (in part): 463–464
Catillicephala rotunda (Rasetti) – Rasetti 1954: 604; Shaw 1966a: 287–288, pl. 34: 24, 25; Palmer in Palmer & Peel 1981: 20, pl. 6: 8, 11, 13

New material. – Numerous disarticulated sclerites in GGU 225528, 225529, 225535, 225537, 225552, 225561, 225563, 225564, 271403, and 271414.

Remarks. – *C. rotunda* has been adequately described by previous authors (see synonymy). It is characterized by a hemispherical glabella and an axis that does not overhang the back margin of the pygidium. A feature not previously reported is the tendency of some late holaspides to develop an incipient median spinule at the back margin of the occipital ring (Fig. 13.1).

Occurrence. – *C. rotunda* is presently known from Canada (Quebec), North Greenland, and the United States (Vermont). Its observed stratigraphic range is from uppermost Middle Cambrian to lowermost Upper Cambrian. It is one of the most common trilobites in the basal part of the Holm Dal Formation, being especially common in lime grainstone.

Genus *Madarocephalus* Resser 1938

Madarocephalus – Resser 1938: 87; Rasetti 1946: 457; Rasetti 1954: 604–606; Rasetti in Harrington et al. 1959: O284

Type species. – *Madarocephalus laetus* Resser 1938, p. 87, pl. 10, figs 51–53.

Remarks. – The generic concept of Rasetti (1946, 1954) is emended here to include specimens with a narrow anterior border on the cranidium. Representatives of *Madarocephalus* are presently known from the United States (Alabama), Canada (Quebec), and North Greenland. They have an observed stratigraphic range from the upper Middle Cambrian (*Lejopyge laevigata* Zone) to the lower Upper Cambrian (*Crepicephalus* Zone).

Madarocephalus scolus n. sp.

Fig. 16.8–10

Holotype. – Cranidium (Fig. 16.10a-c), MGUH 17.225 from GGU 225546.

Material. – Approximately 50 cranidia in GGU 225543, 225546, and 225548.

Diagnosis. – Tiny cranidium with glabella slightly expanding forward. Anterior border narrow. Posterolateral border of fixigena greatly expanded.

Description. – Representatives of *Madarocephalus* known from cranidium; length, exclusive of occipital spine, less than one mm. Glabella unfurrowed, straight sided, and only slightly expanding forward. Occipital ring bearing long, horizontally directed, median spine. Anterior border narrow and of uniform width (sag.), hidden by overhanging glabella in dorsal view. Palpebral lobe short, opposite anterior third of glabella, and close to glabella at anterior end. Fixigena triangular, with well-developed posterior border furrow; length of posterior border exceptionally expanded posterolaterally to about half that of glabella.

Remarks. – Specimens of *M. scolus* differ from those of *M. laetus* and *M. minor* Rasetti 1946, by the presence of a narrow anterior border on the cranidium. They also have less anterior expansion of the glabella, a relatively longer occipital spine, and a much wider posterolateral border on the fixigena.

Cranidia of *M. scolus* are unusually small, their average length being less than half that in either *M. laetus* or *M. minor*. Because of large size ranges in some associated species, the small size of *M. scolus* probably is not the result of postmortem sorting.

Occurrence. – Specimens of *M. scolus* are rare to common in dark lime mudstone and wackestone from about 107 to 119 m above the base of the Holm Dal Formation.

Family Cedariidae Raymond

Genus *Bonneterrina* Lochman 1936

Type species. – *Bonneterrina prima* Lochman 1936, p. 42, pl. 9, figs 1–3.

Bonneterrina sp.

Fig. 15.11, 15

Remarks. – A single cedariid cranidium in GGU 271414 is characterized by a downsloping and subequally divided frontal area, a large and unfurrowed glabella, and an occipital spine of moderate size. Its characters are closely similar to those of *Bonneterrina appalachia* (Walcott 1916a) as reviewed by Rasetti (1965: 102–103, pl. 2: 10–18) as well as those of *B. greenlandica* described by Palmer (in Palmer & Peel 1981: 23–24, pl. 2). However, quite different pygidia have been assigned to *B. appalachia* and *B. greenlandica.*

One small alaform pygidium in GGU 225535 is questionably assigned to *Bonneterrina.* It is characterized by a broad, strongly tapering axis that extends about two-thirds the length of the pygidium. Two axial rings and a terminal piece are poorly defined. A medial broken spot on the anterior ring suggests an original presence of a dorsal spine. A flat, uniform, moderately wide border becomes progressively more upturned from the anterolateral corners to the posterior midline. The front pair of anterior pleural bands is modified distally to form prominent articulating devices and the front two pairs of posterior pleural bands extend across the border furrow and part way onto the border before disappearing.

The general structure of the single pygidium, including a possible anterior ring spine, resembles that of *Shickshockia cristata* Rasetti (1946: pl. 70: 32–40), although the pleural regions are relatively wider and the border is better defined and more upturned. In his review of *Bonneterrina appalachia,* Rasetti (1965: 103) noted similarities between *Shickshockia* and *Bonneterrina* and questioned whether *Shickshockia* should be maintained as a distinct genus. In view of these similarities, it seems possible that the pygidium in hand may be conspecific with the single cranidium that is here designated as *Bonneterrina* sp. Although from different collections, both the cranidium and pygidium are preserved in lime packstone from about 12 and 22 m above the base of the Holm Dal Formation.

Genus *Cedaria* Walcott 1924

Type species. – *Cedaria prolifica* Walcott 1924, p. 55, pl. 10, fig. 6.

Cedaria major n. sp.

Fig. 14.1–7

Holotype. – Pygidium (Fig. 14.4a, b), MGUH 17.193 from GGU 271417.

Material. – More than 200 disarticulated cranidia and pygidia in GGU 271417.

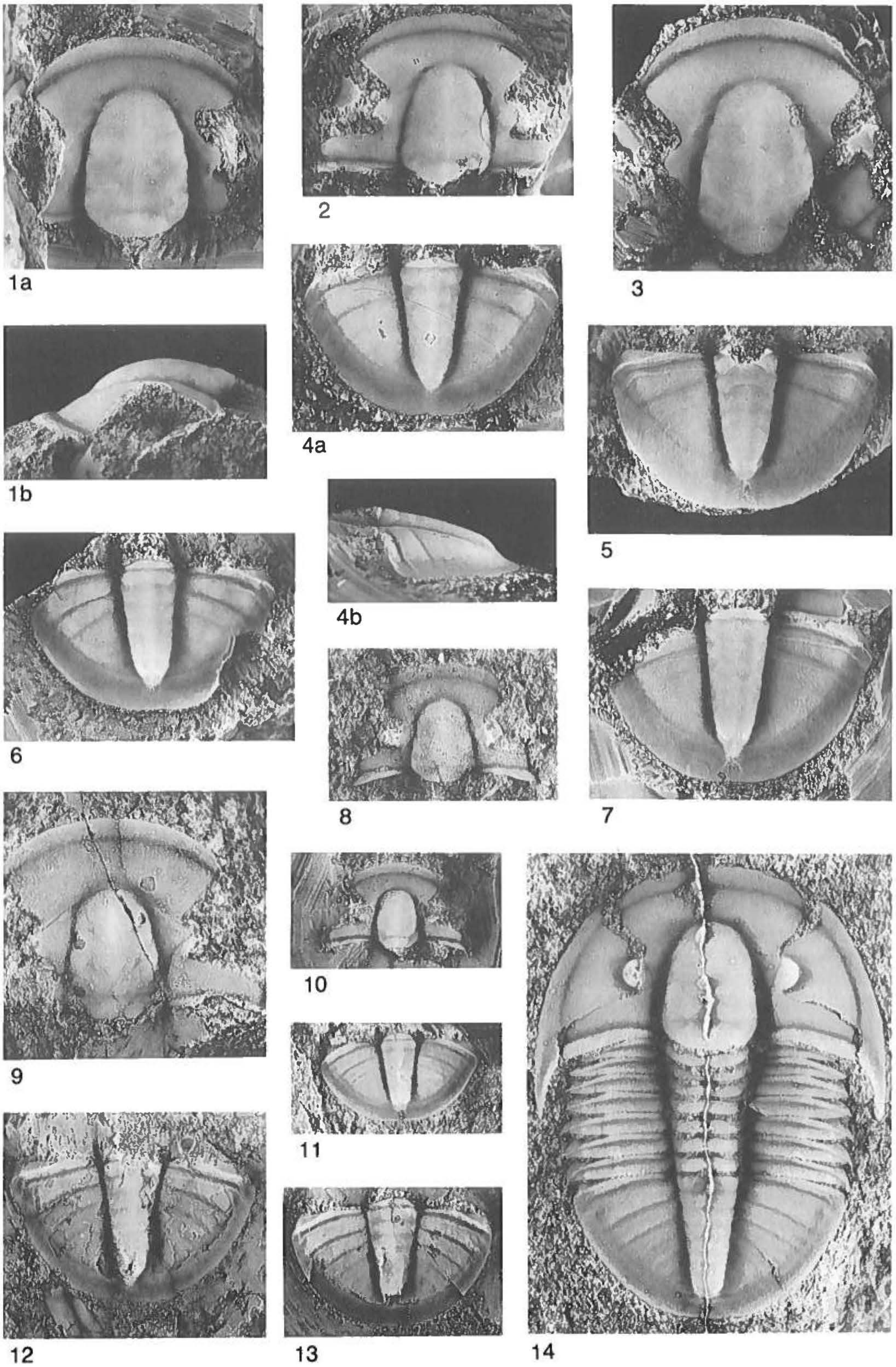
Diagnosis. – Cranidial axis moderately large. Occipital furrow nearly effaced. Palpebral area of fixigena horizontal or slightly upsloping. Pygidium having poorly defined border of moderate width; segmental features weak anteriorly, becoming effaced posteriorly.

Description. – Cranidium having moderately large axis, length of axis about three times that of frontal area. Glabella unfurrowed and broadly rounded anteriorly. Occipital furrow nearly effaced. Frontal area distinctly divided by narrow border furrow, anterior border being about half as long as preglabellar field; lateral margins moderately divergent. Palpebral area of fixigena commonly horizontal; rarely with gentle, upward, abaxial slope. Palpebral lobe small, unelevated or little elevated above fixigena, and opposite glabellar midpoint. Palpebral furrow usually not developed. Posterior fixigena straplike, frontal margin transverse. Length of largest cranidium 12.2 mm.

Pygidium semicircular in outline. Axis moderately well defined with bluntly pointed postaxial ridge extending slightly onto posterior border. Segmental features weakening posteriorly, mostly effaced except vestiges of anteriormost 2 or 3 axial ring furrows and 2 or 3 pairs of pleural furrows. Border moderately wide and poorly defined. Surface of anterior pleural field showing weak venation in low-oblique light.

Remarks. – In maximum size, *C. major* is among the largest species of *Cedaria.* In the late holaspid period it has a proportionately larger cranidial axis than does any previously described species of the genus. Its axis is exceeded in size, however, by that of *C. tumicephala* n. sp., described here. The proportionately large axis is a juvenile character, which suggests a paedomorphic origin for the species. The large holaspid size indicates neoteny rather than progenesis as the paedomorphic process (cf. McNamara 1986).

Cephalic proportions in late holaspides of *C. major* (Fig. 14. 2) resemble those of early holaspides of *C. prolifica* (Fig. 14.10), and probably the two species are closely related. Nevertheless, *C. major* has a significantly wider pygidial border and corresponding doublure, as well as greater effacement of the occipital furrow on the cranidium and pleural furrows on the pygidium.


1a
2
3
1b
4a
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4b
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14

Occurrence. – *C. major* is abundant in a dolomitized trilobite packstone from about 93 m above the base of the Holm Dal Formation. A predominance of large sclerites suggests significant winnowing or current sorting during predepositional transport. The size sorting and matrix also suggest that *C. major* may have lived in a higher energy environment above wave base, whereas coeval *C. prolifica* probably lived in quieter water below wave base.

Cedaria prolifica Walcott 1924

Figs 14.8–14, 26.3

Cedaria prolifica – Walcott 1924: 55, pl. 10: 6; Walcott 1925: 79, pl. 17: 18–21; Palmer 1962: F-26, pl. 3: 9, 10, 14–16, 20, pl. 6: 14 (see for additional synonymy)

New material. – Numerous disarticulated sclerites (GGU 225539–225541, 225543?, 225544, 225546–225548, 225586, 225592–225595, 271404, 315013) and one articulated exoskeleton (MGUH 17.202 from GGU 225541).

Remarks. – A thorough differential diagnosis of this the type species of *Cedaria* has been given by Palmer (1962). Specimens in several collections from the Holm Dal Formation conform in all essential features with that diagnosis.

C. prolifica is characterized by moderately divergent anterior facial sutures, an unfurrowed glabella of moderate size, small and slightly elevated palpebral lobes opposite the glabellar midpoint, lack of palpebral furrows, seven thoracic segments, segmental features of the pygidium that become obscure toward the rear, and a narrow and poorly defined pygidial border. During holaspid ontogeny, length of the preglabellar field increases from about 2 to about 3 times that of the anterior border. Also during ontogeny, the depth of furrows on pleural fields of the pygidium gradually increases; the number of discernible ring furrows increasing from about 5 to 8, and the pairs of pleural furrows from about 3 to 6.

Occurrence. – *C. prolifica* has previously been reported from the lower Upper Cambrian of Alabama, Texas, and Nevada (Palmer 1962). In North Greenland, it is rare to common in lime mudstone and rare in lime wackestone and grainstone, ranging from 25 to 108 m above the base of the Holm Dal Formation. Its occurrence in the upper subzone of the *Lejopyge laevigata* Zone in Greenland is biostratigraphically lower than previously reported. The total observed range of *C. prolifica* is from the upper subzone of the *Lejopyge laevigata* Zone to the *Glyptagnostus stolidotus* (= upper *Crepicephalus*) Zone.

Cedaria tumicephala n. sp.

Fig. 15.1–5

Holotype. – Pygidium (Fig. 15.5a, b), MGUH 17.207 from GGU 271414.

Material. – Five cranidia and 22 pygidia in GGU 225528, 225529, 225535, 225537, 225561, 225563–225565, and 271414.

Diagnosis. – Cranidium tumid; axis proportionately large, axial furrow weak, occipital furrow effaced. Palpebral area of fixigenae downsloping abaxially. Pygidium having weakly defined border of moderate width; segmental features mostly effaced on external surface; postaxial ridge constricted, sharply pointed, extending across most of posterior border.

Description. – Cranidium highly vaulted. Axis weakly defined; proportionately large, being about 3.5 times longer than frontal area. Glabella unfurrowed, broadly rounded anteriorly. Occipital furrow effaced. Frontal area strongly downsloping, anterior border and preglabellar field subequal in length in dorsal view, lateral margins moderately divergent. Palpebral area of fixigena slightly downsloping abaxially. Palpebral lobe small, bounded adaxially by weak palpebral furrow. Posterior fixigena straplike.

Pygidium semicircular in outline. Axis weakly defined, lateral sides having slight inward bow; extending as constricted, sharply pointed postaxial ridge across most of posterior border. Segmental features mostly effaced on dorsal surface; internal mold showing up to 9 axial rings and up to 5 pairs of pleural furrows, all weakly defined. Border moderately wide, border furrow weak.

Fig. 14. *Cedaria major* n. sp. and *Cedaria prolifica* Walcott.

1–7. *Cedaria major* n. sp., all from GGU 271417, all X 3.3. 1, 6. Pathologic cranidium and pygidium; cranidium having malformed right margin of preglabellar field, pygidium showing healed injury of right-posterolateral margin; MGUH 17.189 and 17.190. 2, 3. Fragmentary cranidia, MGUH 17.191 and 17.192. 4. Holotype pygidium in dorsal (a) and left-lateral (b) views, MGUH 17.193. 5, 7. Pygidia, MGUH 17.194 and 17.195.
8–14. *Cedaria prolifica* Walcott. 8–10. Cranidia showing increase in relative sagittal width of preglabellar field with increase in holaspid size; MGUH 17.196–17.198 from GGU 271404, 225539, and 225546, respectively; all X 3.3. 11–13. Pygidia of different holaspid sizes; MGUH 17.199–17.201 from GGU 225546, 225595, and 225544, respectively; all X 3.3. 14. Latex cast of complete dorsal exoskeleton with fracture along midline, MGUH 17.202 from GGU 225541, X 6.

Remarks. – *C. tumicephala* has the largest cranidial axis of any known species of *Cedaria*. In axial size, it is most closely approached by *C. major*. Otherwise, *C. tumicephala* differs from *C. major* by having a fully effaced occipital furrow, a narrower preglabellar field, downsloping fixigenae, and a postaxial ridge that extends further onto the posterior border of the pygidium.

C. tumicephala resembles *C. brevifrons* Palmer 1962, in having a preglabellar field and anterior cranidial border of subequal lengths. However, these species can be easily differentiated by the more general effacement of dorsal furrows in *C. tumicephala*. Also, the palpebral lobes are not elevated in *C. tumicephala* and the pygidium contains at least two more axial rings.

Occurrence. – *C. tumicephala* is rare in lime packstone and grainstone from the basal 22 m of the Holm Dal Formation.

Family Crepicephalidae Kobayashi

Remarks. – The concept and generic content of the Crepicephalidae has varied greatly (e.g. Kobayashi 1935: 275–280; Rasetti 1956: 1269; Lochman in Harrington et al. 1959: O248; Palmer 1962: F27). In general, I concur with the philosophy of Palmer. Here included in the family are *Coosella* Lochman 1936, *Coosia* Walcott 1911, *Coosina* Rasetti 1956, *Crepicephalus* Owen 1852, and *Uncaspis* Kobayashi 1935. This generic assemblage appears to have been derived from ancestors within the Marjumiidae (Robison 1964: 521).

Genus *Crepicephalus* Owen 1852

Type species. – *Dikelocephalus? iowensis* Owen 1852, p. 575, pl. 1, fig. 4; pl. 1A, fig. 13.

Crepicephalus eos n. sp.

Fig. 15.6–10

Holotype. – Pygidium (Fig. 15.9a, b), MGUH 17.211 from GGU 225561.

Material. – Nine cranidia and two pygidia in GGU 225528, 225529, 225547, 225552, and 225561.

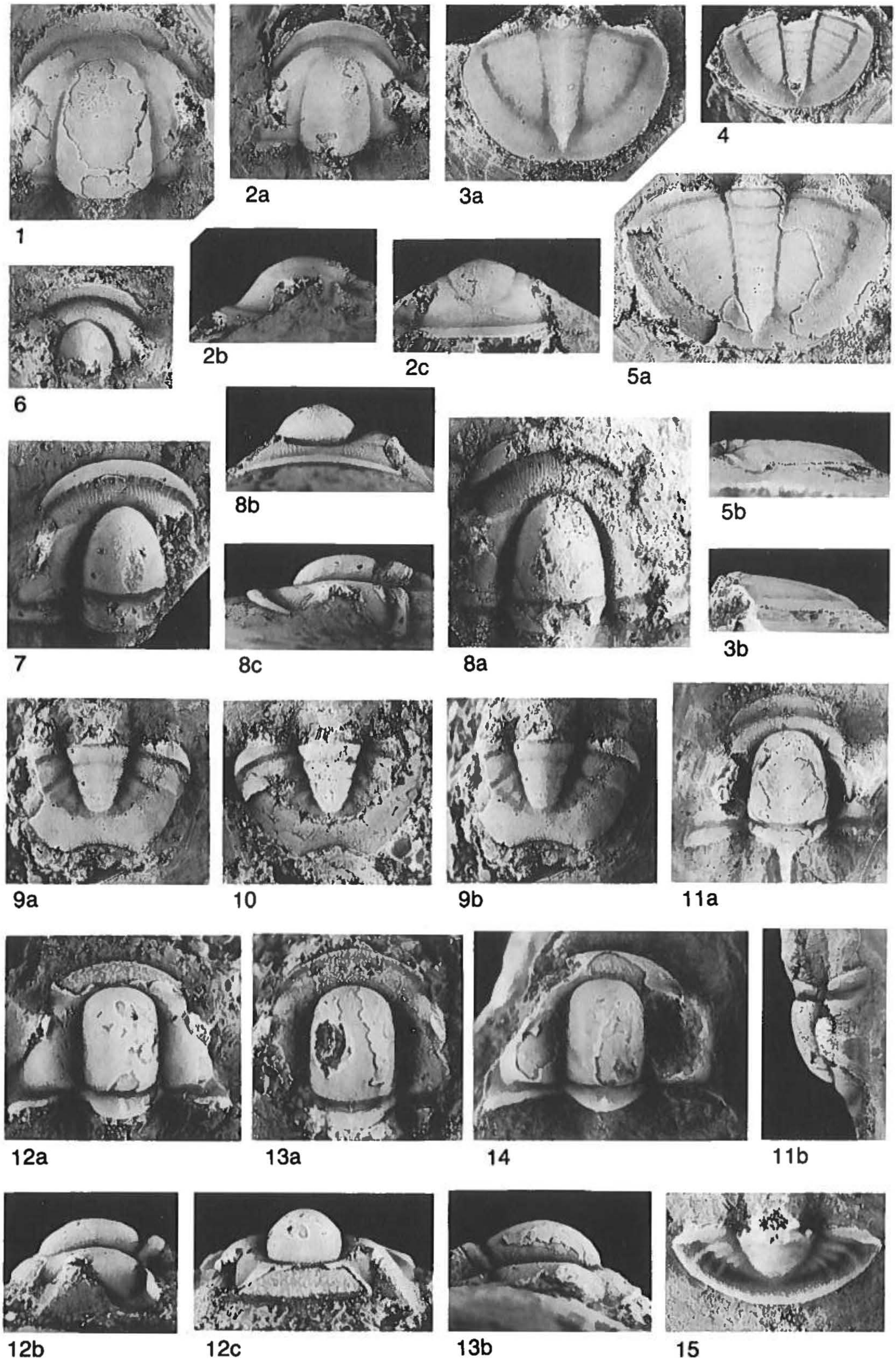
Diagnosis. – Pygidial spines short, obtuse. Glabella ogiviform, unfurrowed. Anterior border furrow of cranidium bearing single string of closely spaced, small pits.

Description. – Cranidium having well-rounded anterior margin. Glabella unfurrowed, moderately elevated above genal region, tapering to narrow rounded front. Occipital furrow moderately wide, bowed slightly backwards. Occipital ring longitudinally wide. Frontal area only slightly downsloping; unequally divided, preglabellar field being 1.4 to 2.0 times wider (sag.) than border; vascular prosopon weakly developed, running forward on preglabellar field; border furrow shallow, containing single string of small, closely spaced pits. Eye ridge weak. Palpebral area of fixigena slightly convex, projecting nearly horizontal. Palpebral lobe about one-third length of glabella, opposite or slightly forward of glabellar midpoint. Anterior facial sutures moderately divergent, straight.

Pygidium having pair of short, broad-based, obtusely pointed spines. Axis evenly and moderately tapering to narrow, rounded end; length about two-thirds that of pygidium on sagittal line; ring furrows weaken toward posterior, two rings being evident on front half of axis. Pleural field narrow, nearly flat; having 3 or 4 furrows that progressively weaken rearward. Border furrow weak, poorly defined; position coincides with inner edge of wide doublure. Border irregularly wide, slightly convex; surface smooth except for continuation of two

Fig. 15. *Cedaria tumicephala* n. sp., *Crepicephalus eos* n. sp., *Bonneterrina* sp. and *Exigua quebecensis* (Rasetti).

1–5. *Cedaria tumicephala* n. sp., all X 3.3. 1. Partly exfoliated, incomplete cranidium, MGUH 17.203 from GGU 271414. 2. Cranidium in dorsal (a), left-lateral (b), and frontal (c) views; MGUH 17.204 from GGU 225563. 3, 4. Pygidia, MGUH 17.205 and 17.206 from GGU 225535 and 271414, respectively. Fig. 5. Holotype pygidium in dorsal (a) and left-lateral (b) views, MGUH 17.207 from GGU 271414.
6–10. *Crepicephalus eos* n. sp., all X 4.4. 6. Anterior fragment of mostly exfoliated, smaller holaspid cranidium, MGUH 17.208 from GGU 225529. 7. Larger cranidium showing pitted anterior border furrow and vascular prosopon on preglabellar field, MGUH 17.209 from GGU 225547. 8. Mostly exfoliated cranidium in dorsal (a), frontal (b), and left-lateral (c) views; MGUH 17.210 from GGU 225561. 9. Holotype pygidium in stereo (a, b) view, MGUH 17.211 from GGU 225561. 10. Pygidium showing mostly exposed doublure, MGUH 17.212 from GGU 225529.
11, 15. *Bonneterrina* sp. 11. Partly exfoliated cranidium in dorsal (a) and left-lateral (b) views, MGUH 17.213 from GGU 271414, X 4.4. 15. Pygidium questionably assigned to *Bonneterrina*, MGUH 17.214 from GGU 225535, X 8.8.
12–14. *Exigua quebecensis* (Rasetti). 12. Partly exfoliated cranidium in dorsal (a), left-lateral (b), and frontal (c) views; MGUH 17.215 from GGU 225552, X 8.8. 13. Exfoliated cranidium in dorsal (a) and right-lateral (b) views showing shallow border furrow and narrow anterior border, MGUH 17.216 from GGU 225528, X 6.6. 14. Partly exfoliated, fragmentary cranidium, MGUH 17.217 from GGU 225535, X 8.8.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anterior pleural furrows; lateral margins convergent on tips of spines.

Remarks. – *C. eos* is the oldest known species of *Crepicephalus* and probably represents the ancestral lineage of the genus. It differs from all other species of *Crepicephalus* by its poorly developed pygidial spines and the pitted border furrow of the cranidium. Most other species also have a more bluntly rounded anterior glabella. In shape of the pygidium, *C. eos* most closely resembles *C. convergens* Rasetti 1965, but it differs in such details as shorter border spines, a wider anterolateral border, and lack of a postaxial ridge.

Occurrence. – Rare in lime grainstone, ranging through the lower 110 m of the Holm Dal Formation.

Family Dolichometopidae Walcott

Genus *Athabaskiella* Kobayashi 1942

Bathyuriscus (Athabaskiella) – Kobayashi 1942: 471
Athabaskiella Kobayashi – Poulsen in Harrington et al. 1959: O222; Palmer 1968: B43-B44

Type species. – *Bathyuriscus (Poliella) probus* Walcott 1916b, p. 354, pl. 65, figs 2, 2', 2a, 2a'.

Emended diagnosis. – Dolichometopid with narrow continuous anterior border on cranidium. Glabella expanding forward in anterior half; having four pairs lateral furrows, S1 deepest and strongly oblique backwards. Palpebral lobe of medium length, slightly posterior from glabellar midpoint. Pygidium cordiform to triangular; axis usually about half pygidial length, having 1 or 2 rings and terminal piece; pleural region concave, border not differentiated; posteromedian margin may be extended (*A. ardis*) into broad, long spine.

Remarks. – *Athabaskiella* most closely resembles *Bathyuriscidella* Rasetti 1948, but differs primarily in having a continuous anterior border on the cranidium, a cordiform or triangular rather than an aliform pygidium, and usually a shorter pygidial axis. *Athabaskiella* also resembles *Bathyuriscus* Meek 1873, in cephalic features, but differs markedly in pygidial structure and relative size of the pygidium.

Representatives of *Athabaskiella* are presently known from the United States (Alaska, New York, Utah, Vermont), Canada (Quebec), and North Greenland. Described species include *A. ardis* Palmer 1968, *A. longicauda* Rasetti 1948, *A. obsoleta* (Raymond 1937), and *A. probus*. A poorly illustrated pygidium of *Bathyuriscidella palauquiana* Rusconi 1955, from Mendoza, Argentina, may represent *Athabaskiella* (Rusconi 1955: 23–24, pl. 1: 16). Probably all North American specimens are from the *Lejopyge laevigata* Zone. New material from Greenland is from the same zone.

Athabaskiella obsoleta (Raymond 1937)

Fig. 16.11–15

Calvinella obsoleta – Raymond 1937: 1090–1091, pl. 1: 18

New material. – Two cranidia, two pygidia, a questionably assigned labrum, and a few questionably assigned thoracic segments in GGU 225535, 315009, 315011, 315012, and ?315013.

Remarks. – *A. obsoleta* previously has been known from only the holotype pygidium. A photograph of that pygidium is figured here (Fig. 16.15) for the first time. Pygidia of *Athabaskiella* from Greenland are smaller than the holotype of *A. obsoleta* but otherwise are almost identical. They differ from pygidia of *A. longicauda* by having more angular anterolateral shoulders.

Occurrence. – Most of the new specimens are preserved in dark lime mudstone from about 26 to 27 m above the base of the Holm Dal Formation in Freuchen Land. One small pygidium is in lime grainstone from about 22 m above the base of the Holm Dal near its type section.

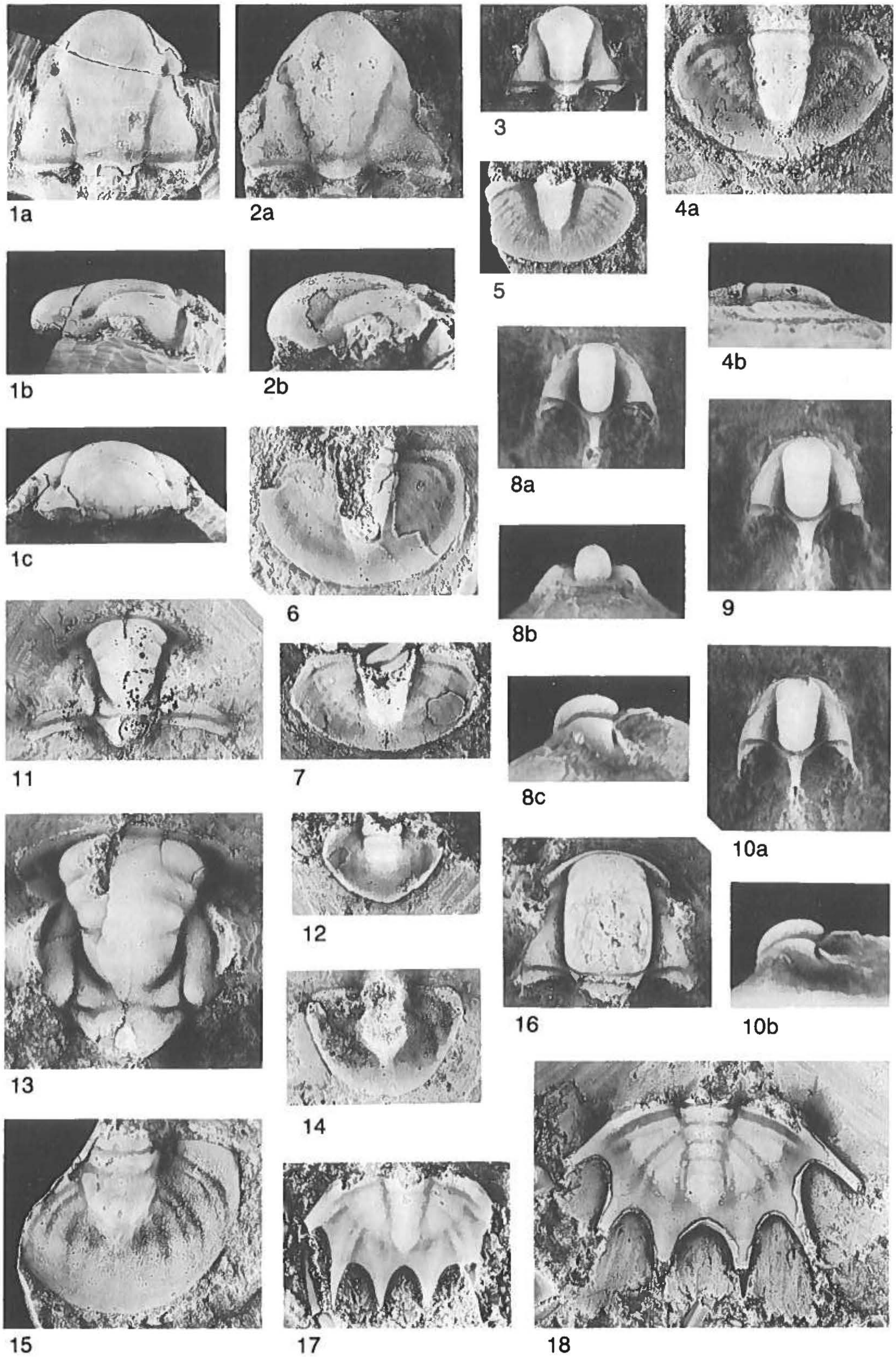
Fig. 16. *Hemirhodon* sp., *Madarocephalus scolus* n. sp., *Athabaskiella obsoleta* (Raymond) and *Olenoides ternus* n. sp.

1–7. *Hemirhodon* sp. 1. Mostly exfoliated, large cranidium in dorsal (a), left-lateral (b), and frontal (c) views, MGUH 17.218 from GGU 225537, X 1.1; note development of anterior snout seen in 1b. 2, 3. Intermediate and small cranidia, MGUH 17.219 and 17.220 from GGU 225561 and 225535, X 3.3 and 5.5, respectively. 4–7. Small pygidia, MGUH 17.221–17.224 from GGU 225561, 225535, 225547, and 225561 respectively, all X 5.5.

8–10. *Madarocephalus scolus* n. sp., all from GGU 225546, all X 16.5. 8. Holotype cranidium in dorsal (a), frontal (b), and left-lateral (c) views, MGUH 17.225. 9, 10. Cranidia, MGUH 17.226 and 17.227.

11–15. *Athabaskiella obsoleta* (Raymond). 11, 13. Cranidia, MGUH 17.228 and 17.229 from GGU 315009 and 315011 respectively, both X 5.5. 12, 14. Pygidia, MGUH 17.230 and 17.231 from GGU 225535 and 315012 respectively, both X 5.5. 15. Holotype pygidium, latex cast; from Rockledge Conglomerate, northwest of Georgia, Vermont; Yale Peabody Museum no. 14708, X 3.3.

16–18. *Olenoides ternus* n. sp. 16. Small cranidium, MGUH 17.232 from GGU 225561, X 8.8. 17. Testaceous pygidium, MGUH 17.233 from GGU 225535, X 4.4. 18. Holotype pygidium, mostly exfoliated; MGUH 17.234 from GGU 271414, X 3.3.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Family Dorypygidae Kobayashi

Genus *Olenoides* Meek 1877

Type species. – *Paradoxides? nevadensis* Meek 1870, p. 62.

Remarks. – The taxonomy of *Olenoides* has been previously reviewed (Robison 1964: 537). More recently, *O. nevadensis* (Meek) was redescribed on the basis of additional topotype specimens (Robison 1971: 799–800, pl. 89: 13–15).

Olenoides ternus n. sp.

Fig. 16.16–18

Holotype. – Pygidium (Fig. 16.18), MGUH 17.234 from GGU 271414.

Material. – Three cranidia and eight pygidia in GGU 225529, 225535, 225561, 225564, 225565, 271403, 271414, and 315013. One poorly preserved, enrolled exoskeleton in 225540 questionably represents this species.

Diagnosis. – *Olenoides* having weakened dorsal furrows on pygidium and three pairs of broad-based pygidial spines of subequal size and spacing.

Description. – Cranidium known from only very small, probably early holaspides, which likely differ in some details from later holaspides. Glabella subparallel sided, unfurrowed except for pair of shallow indentations near anterior end. Occipital ring medially expanded, but presence or absence of spine unknown because of inadequate preservation. Anterior border furrow narrow and well defined where coincident with axial furrow at front of glabella, wide and ill defined across fixigenae. Palpebral lobe short, opposite glabellar midpoint. Posterior area of fixigena relatively long (exsag.) and narrow (tr.).

Pygidium having weakened furrows on dorsal surface. Axis with five rings and terminal piece, mostly effaced except on exfoliated specimens; slightly tapered with minor constriction near boundary between third and fourth rings. Pleural field adaxially convex, passing gradually into concave marginal area. Border spines consisting of three pairs; broad based, subequal in size and spacing; gentle curvature continuing upward from concave marginal area. Corresponding three sets of pleural and interpleural furrows progressively weaken toward posterior.

Remarks. – More than 50 species of *Olenoides* have been named in various parts of the world. To my knowledge, the only previously named species of *Olenoides* with three pairs of marginal spines on the pygidium is *O. trispinosus* Rasetti 1946, which is known from two pygidia (Rasetti 1946: 459–460, pl. 70: 16). *O. ternus* also has three pairs of pygidial spines but differs from *O. trispinosus* by having broader based spines of more uniform size and spacing. In addition, the pygidial axis is evenly tapered in *O. trispinosus* but has a minor constriction at the third ring furrow in *O. ternus*.

In the Holm Dal Formation, the best preserved specimens of *O. ternus* are all relatively small. Fragmentary specimens have a maximum pygidial length of at least 15 mm exclusive of spines.

Occurrence. – Specimens are rare in the lower 50 m of the Holm Dal Formation and are preserved in lithologies varying from dark lime mudstone to light-grey skeletal grainstone. A questionably assigned specimen from about 57 m above the base of the formation is preserved in dark lime mudstone.

Family Kingstoniidae Kobayashi

Genus *Ankoura* Resser 1938

Type species. – *Ankoura triangularis* Resser 1938, pp. 58–59, pl. 9, fig. 33.

Remarks. – The definition of *Ankoura* needs clarification. Rasetti (1965: 61, pl. 3: 15–21) has discussed and provided good illustrations of *A. triangularis*. Cranidia with a very different frontal area and glabellar form have been assigned to *A. apicalis* by Duncan (in Lochman & Duncan 1944), *A. orbiculata* by Lochman (in Lochman & Duncan 1944) and Lochman & Hu (1962), and *A. sublettensis* (Miller 1936) by Lochman & Duncan (1944). Also, cranidia very similar to that of *A. triangularis* have been assigned to *Kingstonia spicata* by Lochman & Hu (1962). Pending further taxonomic study, I provisionally assign specimens from Greenland to *Ankoura* on the basis of their similarity to representatives of the type species and not necessarily similarity to other species that have been assigned to the genus.

Ankoura sp.

Fig. 17.13, 14

Material. – Five fragmentary cranidia in GGU 225552, 225561, and 225563.

Remarks. – Rare cranidia in the Holm Dal fauna closely resemble those of *A. triangularis* except for shape of the posterior fixigena (cf. Rasetti 1965: pl. 3: 19, 20). In these specimens, the posterior fixigenal margin curves sharply backwards near the abaxial end, whereas in *A. triangularis* the margin is transverse or only slightly oblique backwards. The Greenland specimens probably represent a new species, but are left in open nomenclature pending discovery of more and better preserved material.

Occurrence. – Rare in lime grainstone from the basal few metres of the Holm Dal Formation.

Genus *Bynumia* Walcott 1924

Type species. – *Bynumia eumus* Walcott 1924, p. 54, pl. 14, fig. 3.

Bynumia metisensis Rasetti 1946

Fig. 17.1–10

Bynumia metisensis – Rasetti 1946: 448–449, pl. 67: 23–25

New material. – More than 25 cranidia, 10 pygidia, and 3 librigenae in GGU 225528, 225529, 225535, 225552, 225561, 225563, and 271414.

Supplementary diagnosis. – Cranidium subtriangular; rather strongly convex longitudinally and transversely, longitudinal convexity greatest in posterior half. Dorsal furrows mostly or entirely effaced on testaceous specimens; axial furrow shallow, narrow, and distinct on exfoliated specimens. Glabella broad, tapering slightly forward, bluntly rounded anteriorly. Frontal area varying from short and broadly rounded to moderately long and acutely pointed. Anterior and posterior sections of facial suture forming broadly obtuse angle at palpebral lobe. Librigena lacks genal spine.

Pygidium semicircular. Axis slightly elevated above pleural fields; tapering and extending nearly full length of pygidium. Axial segmentation weak on dorsal surface; as many as eight segments indicated by large, paired, lateral muscle scars on exfoliated surface. Pleural field only slightly downsloping. Border narrow but distinct on both testaceous and exfoliated specimens.

Remarks. – Common kingstoniid cranidia in the lower Holm Dal Formation show considerable variation in outline of the frontal area. Most specimens are intermediate in form between typical representatives of *Ankoura* and *Bynumia.* A correlation between holaspid size and general form is not evident. Because the total cranidial aspect is closer to that of *Bynumia,* and associated pygidia are similar to those of *Bynumia,* the cranidia and pygidia are assigned to that genus. Also, because the observed variation in cranidial form encompasses that of the holotype of *B. metisensis,* which has a pointed frontal area, the Holm Dal specimens are assigned to that species. A librigena and pygidium have not previously been described for *B. metisensis.*

In length and shape of frontal area, some cranidia of *B. metisensis* (Fig. 17.2) closely resemble cranidia here assigned to *Ankoura* sp. (Fig. 17.14), but differences in dorsal profile enable differentiation. *B. metisensis* is more convex in the posterior half of the cranidium and its frontal area is less steeply downturned.

Occurrence. – All new specimens of *B. metisensis* are in lime packstone and grainstone from the basal 22 m of the Holm Dal Formation. The species is presently known from Quebec, Canada, and North Greenland.

Genus *Kingstonia* Walcott 1924

Type species. – *Kingstonia apion* Walcott 1924, p. 58, pl. 14. fig. 2.

Kingstonia peltata Palmer in Palmer & Peel 1981

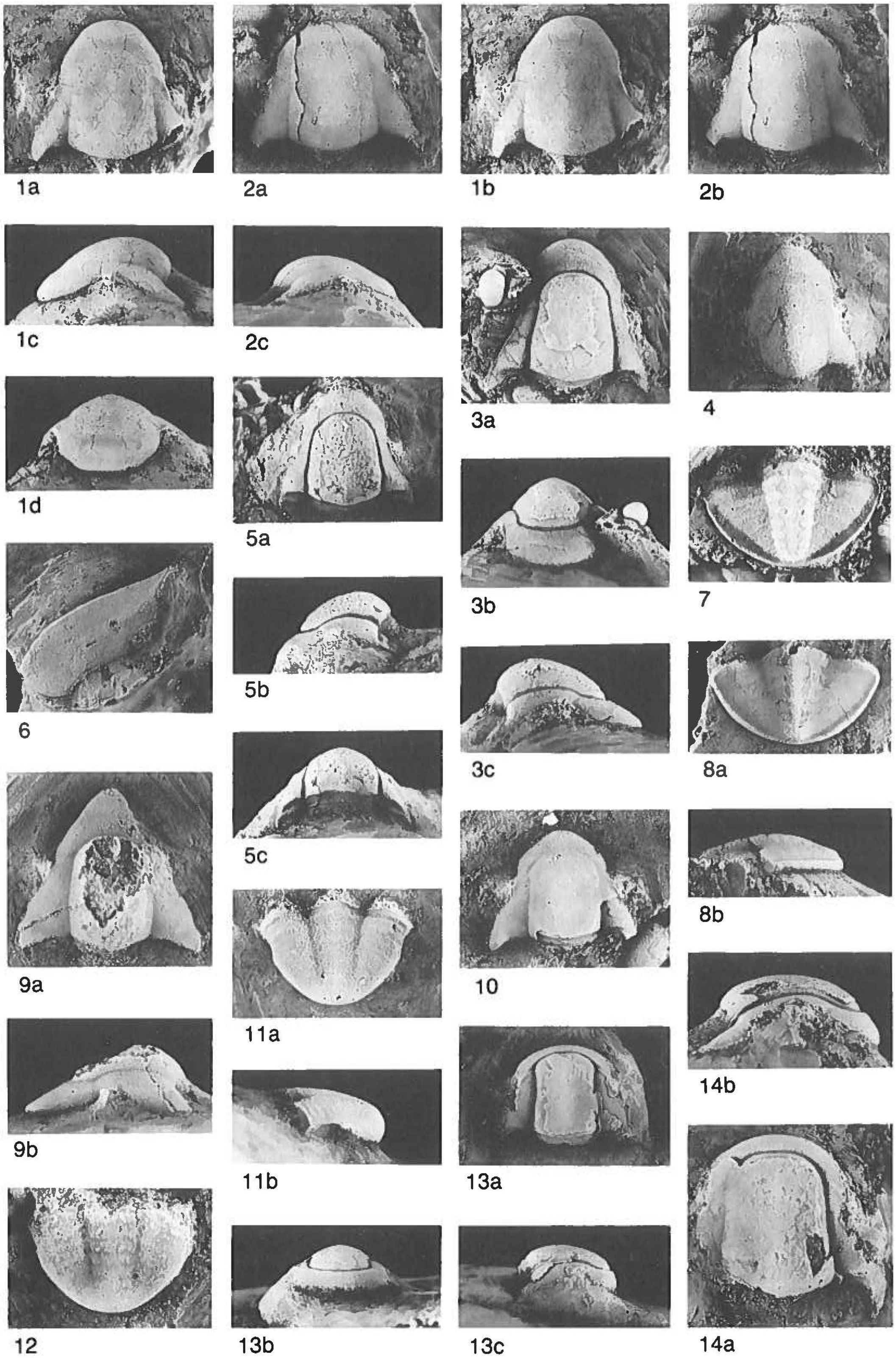
Fig. 17.11, 12

Kingstonia peltata – Palmer in Palmer & Peel 1981: 25, pl. 4: 1–11, 13, 14

New material. – Three pygidia, one in GGU 225563 and two in 225565.

Remarks. – Rare pygidia, preserved as internal molds, possess the distinctive notches on the anterolateral margins that characterize *K. peltata.* The new specimens add no additional morphological information to the original description by Palmer.

Palmer (in Palmer & Peel 1981: 25) suggested that the pygidial notch in *K. peltata* "probably served to accommodate an unusual pleural tip on the last thoracic segment." This would require a "fish-hook" bend near the distal tip of the thoracic segment, and the function or value of such a peculiar structure is difficult to imagine. Horizontal cuticular terraces along the surface of the notch (Palmer & Peel 1981: pl. 4: 10) suggest an alternative explanation for the unusual feature. Schmalfuss (1978, 1981) concluded that the mechanical function of cuticular terraces in trilobites was frictional interaction with the substrate. Schmalfuss further concluded that different terrace patterns on dorsal and ventral surfaces facilitated burrowing and consolidation of walls of the filter chamber beneath the animal, respectively. Alternatively, Savazzi (1985) has shown that cuticular ter-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races in brachyuran decapods increase the friction against the walls of burrows when the animal wedges itself to avoid being extracted by predators. Which of these functions, if any, was served by terraces in the notches of *K. peltata* is undetermined, but the downward facing scarps suggest burrowing.

Occurrence. – *K. peltata* has previously been described from the Cass Fjord Formation of Dresbachian age in western North Greenland. The species is rare in lime packstone from the basal few metres of the Holm Dal Formation.

Family Llanoaspidae Lochman

Genus *Nixonella* Lochman in Lochman & Duncan 1944

Nixonella – Lochman in Lochman & Duncan 1944: 105; Lochman-Balk in Harrington et al. 1959: O312; Hu 1972: 250–251
Torridella – Lochman & Hu 1962: 16

Type species. – *Nixonella montanensis* Lochman in Lochman & Duncan, 1944, pp. 105–106, pl. 13, figs 27–31.

Emended diagnosis. – Cranidium of low to moderate convexity; maximum observed length 4 mm. Glabella large, tapered, broadly rounded in front. Lateral glabellar furrows very weak; S1 concave, oblique backwards; S2 short, transverse. Occipital ring widened medially; occipital furrow deepest near abaxial ends, straight or slightly bowed backwards. Frontal area short; preglabellar field absent or sagitally very narrow; border furrow narrow, well defined, with gentle anterior bow; anterior border moderately wide (sag.). Palpebral area of fixigena 0.4 to 0.5 width of adjacent glabella, slightly convex, horizontal or slightly downsloping. Palpebral lobe short, opposite glabellar midpoint. Eye ridge weak. Posterior area of fixigena having about same transverse width as occipital ring. Anterior sections of facial suture slightly divergent, straight; posterior section extending to or slightly across lateral border furrow before curving sharply backwards to posterior margin.

Pygidium semicircular to subtriangular, posterior margin entire. Axis conical, one-fourth to one-third pygidial width, extending almost to posterior margin; having 5 to 7 rings. Pleural field nearly flat adaxially, steeply downsloping abaxially; having 4 to 6 narrow, slightly curved, pleural furrows that fade onto border; interpleural furrows deepest abaxially. Border narrow, defined more by change in slope than by distinct border furrow.

Remarks. – Only the type species, *N. montanensis,* has previously been assigned to *Nixonella* without question. A new species, *N. furta,* is added here.

The holotype of *N. montanensis* is a cranidium. Hu (1972) concluded that Lochman's original description of the species was based on an incorrectly attributed pygidium, and he assigned pygidia of rather different aspect to the species. Associations of disarticulated cranidia and pygidia in collections from the Holm Dal Formation accord with Hu's conclusion. Also, Hu (1972) considered *Torridella* to be a synonym of *Nixonella,* with which I concur.

Combined characters of the cranidium, especially the glabella, and the pygidium indicate that *Nixonella* is closely related to *Genevievella* Lochman 1936, and *Llanoaspis* Lochman 1938. *Genevievella* seems to have been derived from *Nixonella* and their recognition as separate genera is arbitrary. Species of *Nixonella* tend to have slightly more anterior palpebral lobes, a more curved anterior border furrow on the cranidium, less distally curved pleural furrows on the pygidium, and posterior sections of the facial suture do not invade as far on to the lateral cephalic border.

Nixonella is presently known from the *Cedaria* Zone of Montana and the *Lejopyge laevigata* Zone of North Greenland.

Fig. 17. *Bynumia metisensis* Rasetti, *Kingstonia peltata* Palmer and *Ankoura* sp.

1–10. *Bynumia metisensis* Rasetti. 1, 2. Testaceous cranidia with short and blunt frontal areas, in stereo (a, b) and lateral (c) views; MGUH 17.235 and 17.236 from GGU 225529 and 225561, X 3.3 and 4.4, respectively. 3. Exfoliated cranidium with moderately long and bluntly pointed frontal area, in dorsal (a), frontal (b), and right-lateral (c) views; associated with *Onchonotopsis pergibba* Rasetti (same as pl. 18, Fig. 10); MGUH 17.237 from GGU 225528, X 3.3. 4, 10. Testaceous cranidia having variable frontal areas; MGUH 17.238 and 17.239 from GGU 225561 and 271414, X 4.4 and 5.5, respectively. 5. Exfoliated cranidium in dorsal (a), left-lateral (b), and rear (c) views; MGUH 17.240 from GGU 271414, X 3.3. 6. Left librigena, MGUH 17.241 from GGU 225552, X 4.4. 7. Exfoliated pygidium with serial raised pairs of muscle scars along sides of axis and small pathologic indentation of left anterolateral margin; MGUH 17.242 from GGU 225561, X 4.4. 8. Testaceous pygidium in dorsal (a) and left-lateral (b) views, MGUH 17.243 from GGU 225529, X 4.4. 9. Incomplete, testaceous cranidium having acutely pointed frontal area and glabella better defined than usual; MGUH 17.244 from GGU 225535, X 5.5.
11, 12. *Kingstonia peltata* Palmer, exfoliated pygidia, MGUH 17.245 and 17.246 from GGU 225565 and 225563 respectively, both X 5.5.
13, 14. *Ankoura* sp., exfoliated cranidia in multiple views, MGUH 17.247 and 17.248, both from GGU 225561, and both X 3.3.

Nixonella furta n. sp.

Fig. 18.12–16

Holotype. – Cranidium (Fig. 18.15a, b), MGUH 17.263 in GGU 315009.

Material. – More than 30 cranidia and 7 pygidia in GGU 315007, 315009, and 315011–315013.

Diagnosis. – *Nixonella* having very narrow preglabellar field, anterior border of cranidium nearly flat, palpebral area of fixigena slightly downsloping. Pygidium subtriangular, pleural furrows well impressed. Large, weak, widely spaced granules present on dorsal surfaces of cranidium and pygidium.

Remarks. – Cranidia of *N. furta* closely resemble those of *N. montanensis,* but differ by the presence of a very narrow preglabellar field. Pygidia of the two species are similar in general form, but *N. furta* has a slightly longer axis and furrows are much deeper on the pleural fields.

Occurrence. – Rare to common in dark lime mudstone from about 25 to 50 m above the base of the Holm Dal Formation in Freuchen Land.

Family Lonchocephalidae Hupé.

Genus *Agelagma* Öpik 1967

Type species. – *Agelagma quadratum* Öpik 1967, p. 210, pl. 10, figs 1–3.

Agelagma quadratum Öpik 1967

Fig. 19.10–14

Agelagma quadratum – Öpik 1967: 210, pl. 10: 1–3; text-fig. 72

New material. – Six cranidia in GGU 225561, 271403, and 271414. Also, for comparison, two cranidia and one pygidium from Nevada (R. A. Robison collection 795, University of Kansas).

Remarks. – This small, unusual lonchocephalid is characterized by its quadrate glabella, two pairs of pitlike lateral glabellar furrows, relatively wide fixigena with steeply downsloping posterior area, and lack of an occipital spine. Cranidia from Greenland closely resemble those of *A. quadratum* illustrated by Öpik (1967) from Australia, but are better preserved. The Australian cranidia were described as having a granulose surface texture, but the granulosity is irregular and appears to be a secondary feature resulting from coarse silicification. Cranidia from Greenland have a smooth surface. Öpik's (1967: text-fig. 72) reconstruction also shows a medial node that is well back from the anterior margin of the occipital ring, but all well-preserved specimens have a node located at the anterior margin. The anterior border on cranidia from Greenland varies from being weakly to moderately well defined.

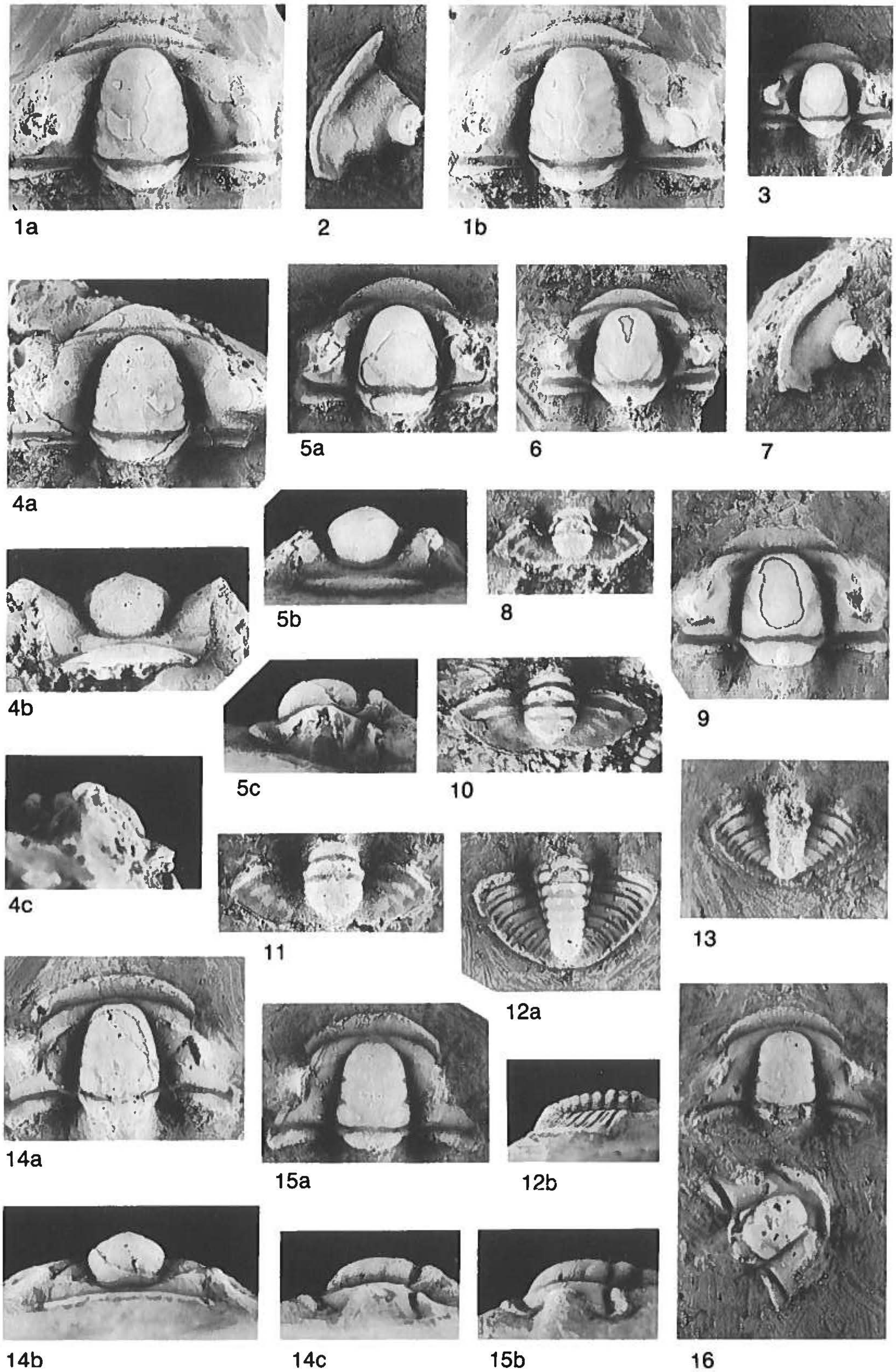
Although previously unreported, rare specimens of *A. quadratum* have been collected from the uppermost bed of the medial limestone marker unit of the Lincoln Peak Formation in the southern White Pine Range, about 4 km north-east of Currant, Nye County, Nevada (R. A. Robison collection 795). A cranidium and pygidium are illustrated (Fig. 19.10, 14) to document the taxonomic occurrence in Nevada and to support a suggestion that this species, although rare, may prove to be a widespread and useful biostratigraphic index.

Several morphological features, small size, and observed geographic distribution all are in accord with an inferred pelagic mode of life for *A. quadratum*. In general morphology it most closely resembles the group designated by Fortey (1985) as sluggish, epipelagic trilobites. Among the more notable similarities are the enhanced axial vaulting, exceptional downward slope and extension of the posterior fixigenae, and small size. The pitlike lateral glabellar furrows correspond to enlarged interior apodemes and suggest increased musculature for associated (swimming?) appendages. In general form, the pygidium of *A. quadratum* (Fig. 19.10) is

Fig. 18. *Pearylandia parva* n. gen. n. sp. and *Nixonella furta* n. gen. n. sp.

1–11. *Pearylandia parva* n. gen. and n. sp. 1. Holotype cranidium in stereo (a, b) view, partly exfoliated; MGUH 17.249 from GGU 225561, X 4.4. 2, 7. Left librigenae, each with visual surface of eye attached; MGUH 17.250 and 17.251 from GGU 225561 and 225537 respectively, both X 7.7. 3. Small holaspid cranidium, MGUH 17.252 from GGU 225535, X 8.8. 4. Large cranidium, mostly exfoliated, in dorsal (a), frontal (b), and right-lateral (c) views; MGUH 17.253 from GGU 225561, X 4.4. 5. Partly exfoliated cranidium in dorsal (a), frontal (b), and left-lateral (c) views; MGUH 17.254 from GGU 225561, X 5.5. 6. 9. Cranidia with only minor exfoliation; MGUH 17.255 and 17.256, both from GGU 225535, and both X 5.5. 8. Small, mostly exfoliated pygidium, MGUH 17.257 from GGU 271414, X 8.8. 10, 11. Exfoliated larger pygidia, MGUH 17.258 and 17.259 from GGU 225528 and 225561 respectively, both X 6.6.

12–16. *Nixonella furta* n. gen and n. sp. 12. Pygidium in dorsal (a) and right-lateral (b) views, MGUH 17.260 from GGU 315009, X 6.6. 13. Damaged pygidium, MGUH 17.261 from GGU 315009, X 8.8. 14. Larger, indifferently preserved cranidium in dorsal (a), frontal (b), and left-lateral (c) views; MGUH 17.262 from GGU 315012, X 6.6. 15. Holotype cranidium in dorsal (a) and left-lateral (b) views; MGUH 17.263 from GGU 315009, X 8.8. 16. Two cranidia, MGUH 17.264 (upper) and 17.265 (lower) from GGU 315009, X 8.8.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16

remarkably similar to Ordovician examples illustrated by Fortey. A notable difference is a much smaller size of eyes than in the Ordovician taxa illustrated by Fortey. Giant eyes, however, are a derived character, being entirely unknown in Cambrian trilobites.

Specimens of *Agelagma* with a more rounded anterior glabella than is typical of *A. quadratum* have been documented in unpublished dissertations on slightly younger faunas from Virginia (Derby 1966: pl. 26: 30, 31) and Utah (Eby 1981: pl. 32: 10–13). Those specimens may represent a new species.

Occurrence. – *A. quadratum* is presently known from Australia (Queensland), North Greenland, and the United States (Nevada). At all localities, representatives of the species are associated with a fauna containing *Lejopyge laevigata*. Although Öpik (1967) interpreted the age of the Australian specimens to be early Late Cambrian, I consider them to be late Middle Cambrian. Specimens are rare in lime packstone and grainstone from the lower 93 m of the Holm Dal Formation.

Genus *Glaphyraspis* Resser 1937

Type species. – *Liostracus parvus* Walcott 1899, pp. 463–464, pl. 65, fig. 6.

Remarks. – The generic concept of Palmer (1965: 50–51) is followed here. With inclusion of *G. alpha* n. sp. the observed stratigraphic range of *Glaphyraspis* is extended substantially downward. The genus now has a total observed range from the upper *Lejopyge laevigata* Zone to the lower *Elvinia* Zone.

Glaphyraspis alpha n. sp.

Fig. 19.1, 2

Holotype. – Cranidium (Fig. 19.1a, b), MGUH 17.266 in GGU 225535.

Material. – Two cranidia in GGU 225535.

Diagnosis. – Small *Glaphyraspis* with stout-based occipital spine. Glabella subrectangular with weak S1 and S2. Dorsal surface mostly lacking granulation.

Description. – Cranidium small; maximum observed length, exclusive of occipital spine, about 2 mm. Glabella subparallel sided, length about one-fourth greater than width; S1 shallow, convex, oblique backwards; S2 shallow, pitlike. Occipital furrow broad, deep; with pair of depressions near axial furrows. Occipital ring having stout-based, median spine. Frontal area short, subequally divided by well-defined, anteriorly bowed border furrow; preglabellar field convex, downsloping; anterior border convex, slightly narrowing laterally. Palpebral area of fixigena about half width of adjacent glabella, moderately convex; on average nearly horizontal. Eye ridge narrow, slightly curved. Palpebral lobe short, anterior of glabellar midpoint. Anterior sections of facial suture slightly convergent. Posterior area of fixigena having broad (exsag.), deep border furrow. Dorsal surface smooth except for fine granulation on back parts of glabella and fixigenae.

Remarks. – *G. alpha* is the oldest known species of *Glaphyraspis*. It differs from all described species of the genus by having an occipital spine. Palmer (1965: 51), however, has reported undescribed spinose specimens of *Glaphyraspis* from the Upper Cambrian of Arizona.

Of the described species of *Glaphyraspis*, *G. alpha* most closely resembles the type, *G. parva* (e.g. Rasetti 1965: pl. 10: 9–17). Both have a glabella with subparallel sides, but the glabella of *G. alpha* is more rounded anteriorly, its lateral glabellar furrows are weaker, and its surface granulation is less developed.

Occurrence. – Specimens of *G. alpha* are preserved in lime grainstone from about 16 m above the base of the Holm Dal Formation.

Genus *Hawkinsia* Rasetti 1965

Type species. – *Hawkinsia minuta* Rasetti 1965, pp. 105–106, pl. 3, figs 22–25.

Hawkinsia? sp.

Fig. 19.3, 4

Remarks. – Two small damaged cranidia in GGU 225561 appear to be closely related to representatives of *Hawkinsia* Rasetti 1965, and *Terranovella* Lochman 1938 (see also Palmer 1965: 51–52). They best accord with Rasetti's description of *Hawkinsia*, but the frontal area is nearly horizontal rather than downsloping, the lateral glabellar furrows are undeveloped rather than weakly impressed, and eye ridges are not prominent. They also accord with much of Palmer's revised description of *Terranovella*, but the glabella is less sunken and has less developed lateral furrows, the occipital ring lacks a spine, and the frontal area is more evenly divided and less downsloping. Because of these morphologic features, small number of specimens, and poor preservation, the two specimens are questionably assigned to *Hawkinsia*. These specimens may have significance in representing the ancestral lineage of *Haw-*

kinsia and *Terranovella*. They are preserved in lime grainstone from the basal part of the Holm Dal Formation.

Genus *Welleraspis* Kobayashi 1935

Type species. – *Liostracus? jerseyensis* Weller 1900, pp. 51–52, pl. 1, figs 1–8

Remarks. – The generic diagnosis of Rasetti (1954: 601) is followed here.

Welleraspis newfoundlandensis Lochman 1938

Fig. 19.5–9

Welleraspis newfoundlandensis – Lochman 1938: 469, pl. 56: 9–11; Rasetti 1954: 601

New material. – Fifteen cranidia and 7 pygidia in GGU 225535, 225537, 225540, 225543, 225547, 225552, 225561, 225565, 271408, 271414, and 315007.

Emended diagnosis. – Cranidium moderately convex. Glabella subrectangular to subquadrate; S1 moderately deep, concave, oblique backwards; S2 shallow to moderately deep, straight, transverse. Occipital furrow broad; deeply impressed at sides, shallow medially. Occipital ring triangular, extending backwards into spine of variable length; median node may be present at base of occipital spine. Frontal area short, subequally divided into concave preglabellar field and upturned border; border furrow moderately bowed forward. Palpebral area of fixigena slightly convex, on average near horizontal; width about one-third that of adjacent glabella. Palpebral lobe short, anterior of glabellar midpoint. Posterior fixigena marked by broad, deep border furrow.

Pygidium subtriangular. Axis extending to posterior margin; having 4 rings and long terminal piece. Pleural field downsloping; 4 pleural furrows well impressed; interpleural furrows short, impressed only adjacent to border furrow. Border narrow, entire.

Remarks. – Specimens of *Welleraspis* from the Holm Dal Formation show considerable variation in convexity and outline of the glabella. Most are moderately convex and subrectangular, but grade to higher convexity and a subquadrate outline in some larger holaspides. Depth of the S2 furrows is also variable, as is sagittal width of the anterior cranidial border. Similar variation is evident in other species of *Welleraspis*, having been attributed to sexual dimorphism for some (Hu 1964, 1968, 1969).

The rare cranidia with a quadrate glabella are indistinguishable from *W. newfoundlandensis*, which was originally described from a single cranidium (Lochman 1938). Because of apparent character gradation among the specimens of *Welleraspis* from Greenland, all are provisionally assigned to that species.

A number of synonyms seem to be present among the several described species of *Welleraspis*, but review of types is not possible at this time. The anterior glabella of *W. newfoundlandensis* is more rounded than in most species of the genus, and may indicate a phyletic position near the transition from *Lonchocephalus* Owen 1852, the inferred ancestral lineage of *Welleraspis* (Rasetti 1954: 600).

Occurrence. – *W. newfoundlandensis* is known from western Newfoundland (*Cedaria* Zone) and North Greenland. It ranges through the lower 111 m of the Holm Dal Formation and is rare in a variety of carbonate lithofacies.

Family Marjumiidae Kobayashi

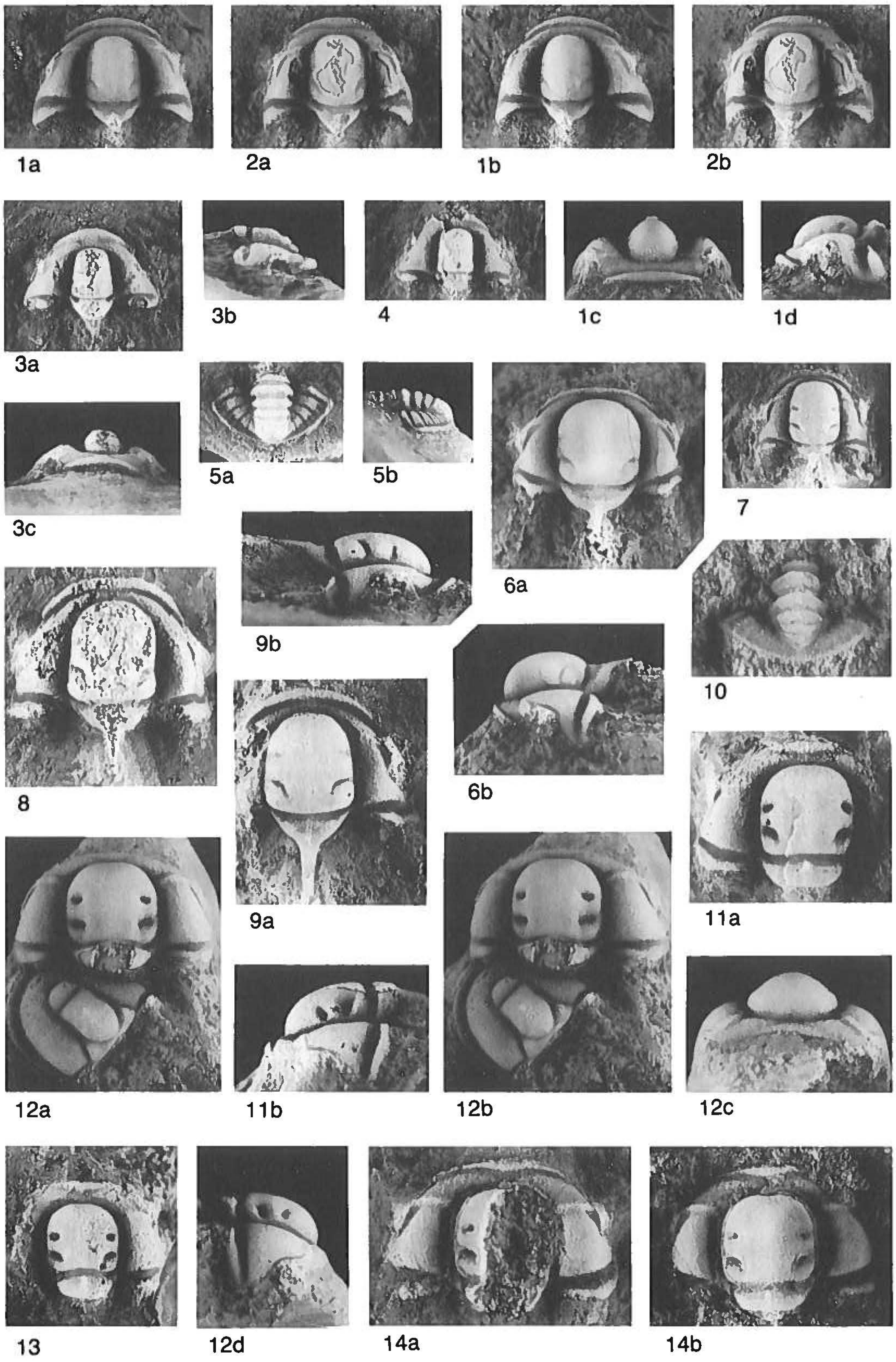
Emended diagnosis. – Relatively simple opisthoparian polymeroids characterized by a tapered, anteriorly rounded glabella. Muscle scars ordinarily present instead of lateral glabellar furrows. Frontal area short; anterior border well developed, preglabellar field absent to subequal to border in sagittal length. Thorax commonly with 13 or 14 segments. Pygidium semicircular to alaform; axis stubby, with 2 to 4 rings and terminal piece. Exoskeleton thicker than average for polymeroids.

Remarks. – This diagnosis is slightly modified from that of Robison (1964: 521, 547). Presently included genera are *Marjumia* Walcott 1916b, *Ithyektyphus* Shaw 1956, *Modocia* Walcott 1924, *Pearylandia* n. gen., *Syspacheilus* Resser 1938, *Talbotina* Lochman 1938, and questionably *Arapahoia* Miller 1936, and *Glyphopeltis* Deiss 1939. Although rare elsewhere (e.g. Rushton 1978: 267–269), representatives of the family are mostly confined to North America and Greenland. The observed stratigraphic range of the family is from the uppermost *Ptychagnostus praecurrens* Zone to an undetermined level in the lower Upper Cambrian.

Genus *Marjumia* Walcott 1916b

Marjumia – Walcott 1916b: 401; Robison 1964: 547–548 (for synonymy to date)

Type species. – *Marjumia typa* Walcott 1916b, p. 402, pl. 65, figs 4, 4a, 4b.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14b

Emended diagnosis. – Marjumiids having spinose pygidial margin and relatively narrow palpebral area of fixigena. Axial furrow deep. Glabella having complex muscle scars. Occipital ring simple or spinose. Preglabellar field absent to subequal to anterior border in sagittal length. Palpebral lobe of moderate length, palpebral furrow shallowing at midlength. Thorax containing 14 segments. Pygidium semicircular; axis broad, bluntly terminated.

Remarks. – A more detailed diagnosis of *Marjumia* (Robison 1964: 547) is slightly modified to include some specimens having occipital spines and some lacking a preglabellar field. To the previously described species *M. callas* Walcott 1916b, and *M. typa* Walcott 1916b, are added here two new species, *M. brevifrons* and *M. spinosa*. A rostral plate, previously unknown in the genus, is described for *M. spinosa*.

Available material, some in undescribed collections, indicates that representatives of *Marjumia* are widely distributed in open-shelf lithofacies of late Middle Cambrian age *(Ptychagnostus punctuosus* to *L. laevigata zones)* in North America and Greenland.

Marjumia brevifrons n. sp.

Fig. 20.1–7

Holotype. – Pygidium (Fig. 20.6), MGUH 17.284 from GGU 225537.

Material. – More than 50 disarticulated sclerites in GGU 225528, 225529, 225535, 225537, 225540, 225552, 225561, 225564, 271403, and 271414.

Diagnosis. – Preglabellar field absent or barely developed. Anterior cranidial border expanded posteromedially. Occipital ring having posteromedial tubercle or short spine. Genal spine stout based and of moderate length. Pygidium with one pair of short anterolateral spines, axis having two rings and long terminal piece.

Description. – Cranidium of moderate convexity. Glabella elongate, little elevated above genae; slightly tapered, well rounded anteriorly; complex muscle scars generally become more evident during holaspid ontogeny. Occipital ring having median tubercle or short spine near posterior margin. Frontal area unequally divided; preglabellar field absent or barely developed; middle part of border furrow commonly having slight backward bow; anterior border slightly convex, expanded posteromedially. Palpebral lobe opposite or slightly posterior of glabellar midpoint. Anterior facial suture slightly divergent; posterior suture strongly divergent, sinuous.

Librigena having stout-based genal spine of moderate length. Border furrow shallowing posteriorly.

Labrum and thorax unknown.

Pygidium semicircular in outline. Axis broad, little tapered, bluntly terminating near posterior pygidial margin; containing two rings and long terminal piece. Anterior pleural furrow well developed. Succeeding furrows of pleural field mostly effaced. Margin smooth except for one pair of short, anterolateral spines.

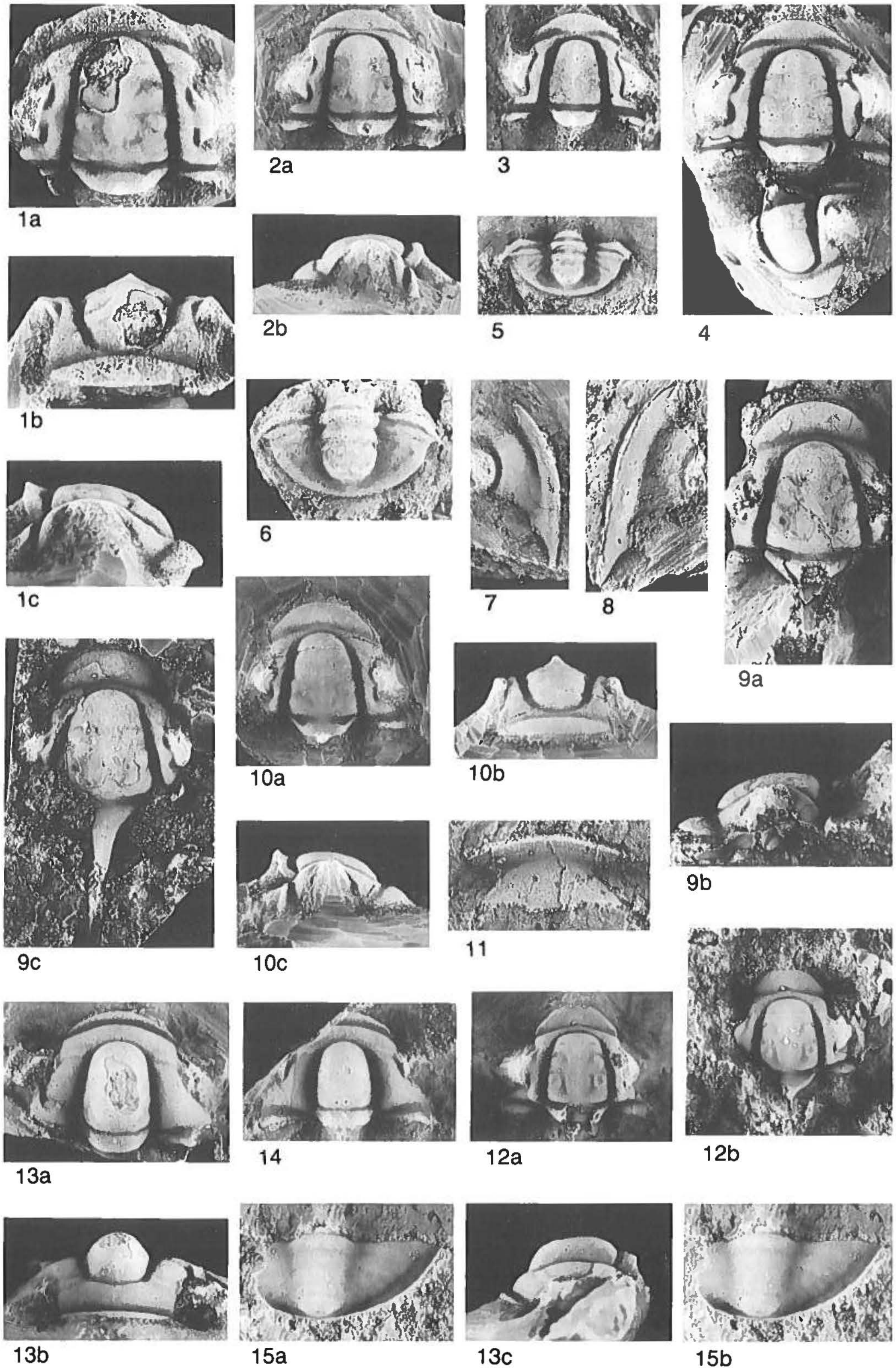
Cephalic surface finely granulose except in furrows and on muscle scars. Pygidial surface finely pitted and with fine granules on marginal areas. Terrace lines sparse and weak around cephalic and pygidial margins.

Remarks. – The pygidium of *M. brevifrons* closely resembles that of *M. callas* (cf. Robison 1964: pl. 86: 20, 21). These species, however, differ by the much reduced preglabellar field, a posteromedial expansion of the anterior cranidial border, narrower palpebral area of fixigena, and presence of a prominent occipital tubercle or short spine in *M. brevifrons*.

M. brevifrons differs from *M. typa* by having a shorter preglabellar field, a posteromedial expansion of the anterior cranidial border, and one rather than three pairs of spines on the pygidial border.

Fig. 19. *Glaphyraspis alpha* n. sp., *Hawkinsia?* sp., *Welleraspis newfoundlandensis* (Lochman) and *Agelagma quadratum* Öpik.

1, 2. *Glaphyraspis alpha* n. sp. 1. Holotype cranidium in stereo (a, b), frontal (c), and left-lateral (d) views; MGUH 17.266 from GGU 225535, X 8.8. 2. Partly exfoliated cranidium in stereo (a, b) view, MGUH 17.267 from GGU 225535, X 8.8.
3, 4. *Hawkinsia?* sp. 3. Cranidium with damaged glabella, in dorsal (a), right-lateral (b), and frontal (c) views, MGUH 17.268 from GGU 225561, X 8.8. 4. Small, partly exfoliated crandium, MGUH 17.269 from GGU 225561, X 8.8.
5–9. *Welleraspis newfoundlandensis* (Lochman). 5. Pygidium in dorsal (a) and left-lateral (b) views, MGUH 17.270 from GGU 225535, X 8.8. 6. Cranidium with highly convex, subquadrate glabella in dorsal (a) and left-lateral (b) views; MGUH 17.271 from GGU 225535, X 11. 7. Smaller cranidium, MGUH 17.272 from GGU 271408, X 8.8. 8. Larger, damaged cranidium, MGUH 17.273 from GGU 225561, X 8.8. 9. Cranidium with moderately convex, subrectangular glabella in dorsal (a) and right-lateral (b) views; MGUH 17.274 from GGU 271414, X 7.7.
10–14. *Agelagma quadratum* Öpik, all X 8.8. 10. Latex cast of pygidium from the uppermost part of the middle limestone member, Lincoln Peak Formation, southern White Pine Range, Nevada; University of Kansas Museum of Invertebrate Paleontology no. 204786. 11. Cranidium in dorsal (a) and left-lateral (b) views, MGUH 17.275 from GGU 225561. 12. Cranidium resting on a cephalon of *Ammagnostus beltensis*, in stereo (a, b), frontal (c), and right-lateral (d) views; MGUH 17.276 from GGU 271417. 13. Cranidium, MGUH 17.277 from GGGU 225561. 14. Damaged cranidium (a), mostly exfoliated, and latex cast from counterpart (b); preserved in dark, recrystallized, lime mudstone from the uppermost part of the middle limestone member, Lincoln Peak Formation, southern White Pine Range, Nevada; University of Kansas Museum of Invertebrate Paleontology no. 204787.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13c
15b

Occurrence. – *M. brevifrons* is rare to common in lime grainstone and rare in lime mudstone and wackestone of the lower 55 m of the Holm Dal Formation.

Marjumia spinosa n. sp.

Fig. 20.4, 8–12

Holotype. – Cranidium (Fig. 20.9a-c), MGUH 17.287 from GGU 225563.

Material. – More than 20 cranidia, several librigenae, and 2 rostral plates in GGU 225529, 225547, 225563, 225565, 271414, and 315013.

Diagnosis. – Preglabellar field barely developed. Occipital ring having prominent posteromedian spine. Lateral border of librigena wide.

Description. – Cranidium of moderate convexity. Glabella little elevated above genae; moderately tapered, anterior end changing from bluntly to moderately rounded during holaspid ontogeny; muscle scars weak. Occipital ring having prominent posteromedian spine, relative size increasing during holaspid ontogeny. Frontal area unequally divided; preglabellar field barely developed; border furrow having fairly uniform, slight forward arc; anterior border wide. Palpebral area of fixigena narrow. Palpebral lobe opposite glabellar midpoint. Anterior facial suture slightly divergent, straight; posterior suture strongly divergent, sinuous. Librigena having relatively wide lateral border.

Rostral plate having moderately deep lateral notches. Maximum lateral width about 2.5 times sagittal length. Anterior margin gently curved. Larger posterior portion bending downward and backward. Posterior margin straight along middle third, probably adjoining anterior margin of labrum; outer margins nearly straight but slightly offset forward.

Remarks. – *M. spinosa* differs from all other species of *Marjumia* by having a prominent occipital spine and wide cephalic border. Otherwise, it most closely resembles *M. brevifrons,* but further differs from that species by lacking the posteromedial expansion of the anterior cranidial border. Pygidia of *M. spinosa* have not been positively differentiated, although they are probably present in association with pygidia of the more common *M. brevifrons.*

All specimens of *M. spinosa* are preserved in limestone. When the limestone matrix is broken, the large, upward-projecting spine and the central part of the occipital ring are commonly broken off (Fig. 20.12). Nevertheless, it usually is possible to differentiate the cranidia from those of associated *M. brevifrons* by differences in shape of the anterior border.

Occurrence. – *M. spinosa* is rare in some lime mudstone, packstone, and grainstone in the lower 111 m of the Holm Dal Formation.

Genus *Modocia* Walcott 1924

Type species. – *Arionellus (Crepicephalus) oweni* Meek & Hayden 1861, p. 436.

Remarks. – Except for emendation to include forms having an unequally divided frontal area of the cranidium, the generic diagnosis of Robison (1964: 550–551) is followed here.

Modocia planata n. sp.

Fig. 21.1–9

Holotype. – Cranidium (Fig. 21.4a-c), MGUH 17.297 from GGU 225561.

Material. – More than 50 disarticulated sclerites in GGU 225528, 225529, ?225533, 225535, 225537, 225540, 225547, 225552, 225561, 225563, 225564, 225592, 271403, and 271414.

Fig. 20. *Marjumia brevifrons* n. sp., *Marjumia spinosa* n. sp., *Elrathia marjumi* Robison and undetermined pygidium.

1–7. *Marjumia brevifrons* n. sp. 1, 2. Cranidia in dorsal (a) and other views; MGUH 17.278 and 17.279, both from GGU 225537, both X 3.3. 3. Small exfoliated cranidium, MGUH 17.280 from GGU 225535, X 5.5. 4. Mostly exfoliated cranidium (upper), associated with cranidium of *Marjumia spinosa* n. sp. (lower); MGUH 17.281 and 17.282 respectively, from GGU 271414, X 3.3. 5. Pygidium, MGUH 17.283 from GGU 225535, X 2.2. 6. Holotype pygidium, MGUH 17.284 from GGU 225537, X 2.2. 7. Right librigena, MGUH 17.285 from GGU 225537, X 3.3.

8–12. *Marjumia spinosa* n. sp. 8. Left librigena, MGUH 17.286 from GGU 225565, X 4.4. 9. Holotype cranidium, mostly exfoliated, in dorsal (a, c) and left-lateral (b) views; 9c is latex cast of counterpart showing partially excavated occipital spine; MGUH 17.287 from GGU 225563, X 2.2. 10. Exfoliated cranidium in dorsal (a), frontal (b), and right-lateral (c) views; MGUH 17.288 from GGU 271414, X 2.2. 11. Rostral plate in exterior view, MGUH 17.289 from GGU 225565, X 5.5. 12. Small, finely granulose, holaspid cranidium with broken occipital ring (a), and latex cast of counterpart with whole occipital ring (b); MGUH 17.290 from GGU 271414, both X 5.5.

13, 14. *Elrathia marjumi* Robison. 13. Cranidium with damaged glabella, in dorsal (a), frontal (b), and left-lateral (c) views; MGUH 17.291 from GGU 315011, X 6.6. 14. Smaller cranidium, MGUH 17.292 from GGU 315011, X 8.8.

15. Undetermined pygidium, incomplete pygidium in stereo (a, b) view, MGUH 17.293 from GGU 225547, X 8.8.

Diagnosis. – Preglabellar field distinctly shorter than anterior cranidial border. Glabella elongate, top nearly flat in lateral profile. Genal spine of moderate length. Posterior margin of pygidium, in posterior view, having broad, angular dorsal arch.

Description. – Cranidium of low convexity, axis barely elevated above genal regions. Glabella elongate, slightly tapered forward, strongly rounded anteriorly; top nearly flat in lateral profile; lateral furrows lacking, muscle scars weak. Occipital ring having weak median node. Frontal area moderately downsloping, unequally divided; preglabellar field approximately one-half width (sag.) of anterior border; border furrow weakly bowed forward, having pair of shallow and wide (tr.) depressions approximately on line with lateral axial furrows. Anterior arch broad and very low. Palpebral area of fixigena slightly convex, moderately wide, only slightly upsloping. Palpebral lobe slightly posterior of glabellar midpoint. Librigena having well-developed border of moderate width, genal spine of moderate length. Anterior facial suture parallel to slightly divergent; posterior suture strongly divergent, sinuous. Surface of test may be weakly granulated, especially along posterior occipital ring.

Pygidium semicircular to alate. Axis stout, little tapered, bluntly terminated, usually having median depression at back end; width slightly wider than pleural regions. Anterior ring, pleural, and interpleural furrows prominent; succeeding furrows becoming progressively shallower; 2 or 3 axial rings usually evident. Border narrow, poorly defined; mostly delineated by termination of pleural and interpleural furrows. Posterior margin in dorsal view commonly having weak, medial, anterior bow; in posterior view showing broad, angular, dorsal arch.

Remarks. – Phylogenetically, *M. planata* is a late species of *Modocia*. It differs from all previously described species of the genus in the combination of its short preglabellar field, elongate glabella, and angular dorsal arch of the posterior pygidium.

Among the fauna of the Holm Dal Formation, cranidia of *Modocia planata* superficially resemble those of *Marjumia brevifrons* n. sp. *M. planata*, however, has a wider palpebral area of the fixigena, a better developed preglabellar field, and lacks a medial expansion of the anterior border.

Occurrence. – *M. planata* is rare to common in the lower 111 m of the Holm Dal Formation. It is most common in lime grainstone and is rare in lime mudstone and packstone.

Genus *Pearylandia* n. gen.

Type species. – *Pearylandia parva* n. sp.

Diagnosis. – Marjumiids having deep axial furrow on cranidium. Glabella large, extending to or almost to anterior border furrow. Palpebral area of fixigena moderately upsloping. Palpebral lobe opposite or posterior of glabellar midpoint. Genal spine stubby or vestigial. Pygidium short, alate with two axial rings and no spines.

Description. – Smaller than average marjumiids, maximum observed cranidial length 6 mm. Axial furrow deep and wide at sides of glabella, shallow and narrow at front. Glabella large, long, moderately convex; sides slightly converging forward, front strongly rounded. Occipital ring having median node. Frontal area short, border furrow shallow with slight forward curve; preglabellar field absent or sagittally very narrow; border gently downsloping, lateral ends acute. Palpebral area of fixigena about one-third width of adjacent glabella, moderately upsloping. Palpebral lobe about one-third length of glabella, wide and flaplike; opposite or posterior to glabellar midpoint. Transverse width of posterior area of fixigena slightly less than that of occipital ring. Eye ridge strongly oblique backwards, weakening abaxially. Anterior sections of facial suture subparallel in front of palpebral lobes, then oblique across border; posterior sections strongly divergent or transverse. Librigena retaining visual surface of eye, but individual lenses not distinguishable beneath cornea; genal spine stubby or vestigial; lateral border furrow weakens backwards, becoming effaced posteriorly.

Pygidium alate; length (exclusive of articulating half ring) about one-third width. Axis broad, extending almost to posterior margin; anterior ring bounded by prominent articulating and first ring furrows, second ring defined posteriorly by weak second ring furrow, terminal piece broadly rounded posteriorly. Pleural field about same width as axis, broadly convex; anterior pleural furrow wide, shallow; other evidence of segmentation mostly effaced. Border narrow, weakly defined. Posterior margin smooth, having low dorsal arch.

Remarks. – *Pearylandia* can be differentiated from other marjumiid genera by the combination of its much reduced or absent preglabellar field, more upsloping palpebral area of the fixigenae, and its short, alaform pygidium. On the basis of comparative morphology and stratigraphic position, *Pearylandia* seems to have been derived directly from *Modocia*, which is the ancestral marjumiid genus.

Representatives of *Pearylandia* are known from Alaska and North Greenland. All are from the *Lejopyge laevigata* Zone.

Pearylandia parva n. sp.

Fig. 18.1–11

Genus and species undetermined 9 – Palmer 1968 (in part): B104, pl. 6: 23 (not 22)

Holotype. – Cranidium (Fig. 18.1a, b), MGUH 17.249 from GGU 225561.

New material. – Numerous specimens in GGU 225528, 225529, 225535, 225537, 225552, 225561, 225563–225565, 271403, 271414, 271417, and 315013.

Description. – Characters of genus.

Remarks. – *Pearylandia parva* is one of the most commonly represented species in the Holm Dal Formation. During holaspid ontogeny the anterior end of the glabella became more strongly rounded, a very narrow preglabellar field developed, slope of the palpebral area of the fixigena steepened, the palpebral lobes migrated rearward, and sections of the facial suture on the anterior cephalic border became more oblique causing lateral ends of the anterior cranidial border to become more acute.

From Alaska, Palmer (1968: B104, pl. 6: 22, 23) has described and illustrated two cranidia as 'Genus and species undetermined 9.' One cranidium (Geological Survey of Canada 20267) appears to represent *Pearylandia,* as here defined, and is tentatively reassigned to *P. parva.* The other cranidium (GSC 20266) is significantly larger, has a somewhat different glabellar outline, large scattered granules, and the posterior area of the fixigena is transversely wider than the occipital ring. In my opinion, the two cranidia are not congeneric, and the latter remains generically unassigned.

Occurrence. – The Alaskan specimen of *P. parva* is probably from the lower *Lejopyge laevigata* Zone and is probably slightly older than specimens from Greenland. The species is one of the most common polymeroids in the lower 93 m of the Holm Dal Formation. It is present in most lithofacies, but is most common in lime grainstone.

Genus *Syspacheilus* Resser 1938

Type species. – *Syspacheilus typicalis* Resser 1938, pp. 99–100.

Remarks. – *Syspacheilus* is known from only disarticulated sclerites. The holotype of *S. typicalis* is a cranidium. Assignments of three quite different kinds of pygidia to either the holotype of *S. typicalis* or to similar cranidia have resulted in very different concepts of *Syspacheilus* (e.g. Resser 1938: 99–100; Palmer 1955: 734; Lochman & Hu 1961: 133–134). Associations of cranidia and pygidia in collections from Greenland support the emended description of the genus by Lochman & Hu, which is followed here.

Syspacheilus catatate n. sp.

Fig. 21.10–14

Holotype. – Pygidium (Fig. 21.12a-c), MGUH 17.305 from GGU 225564.

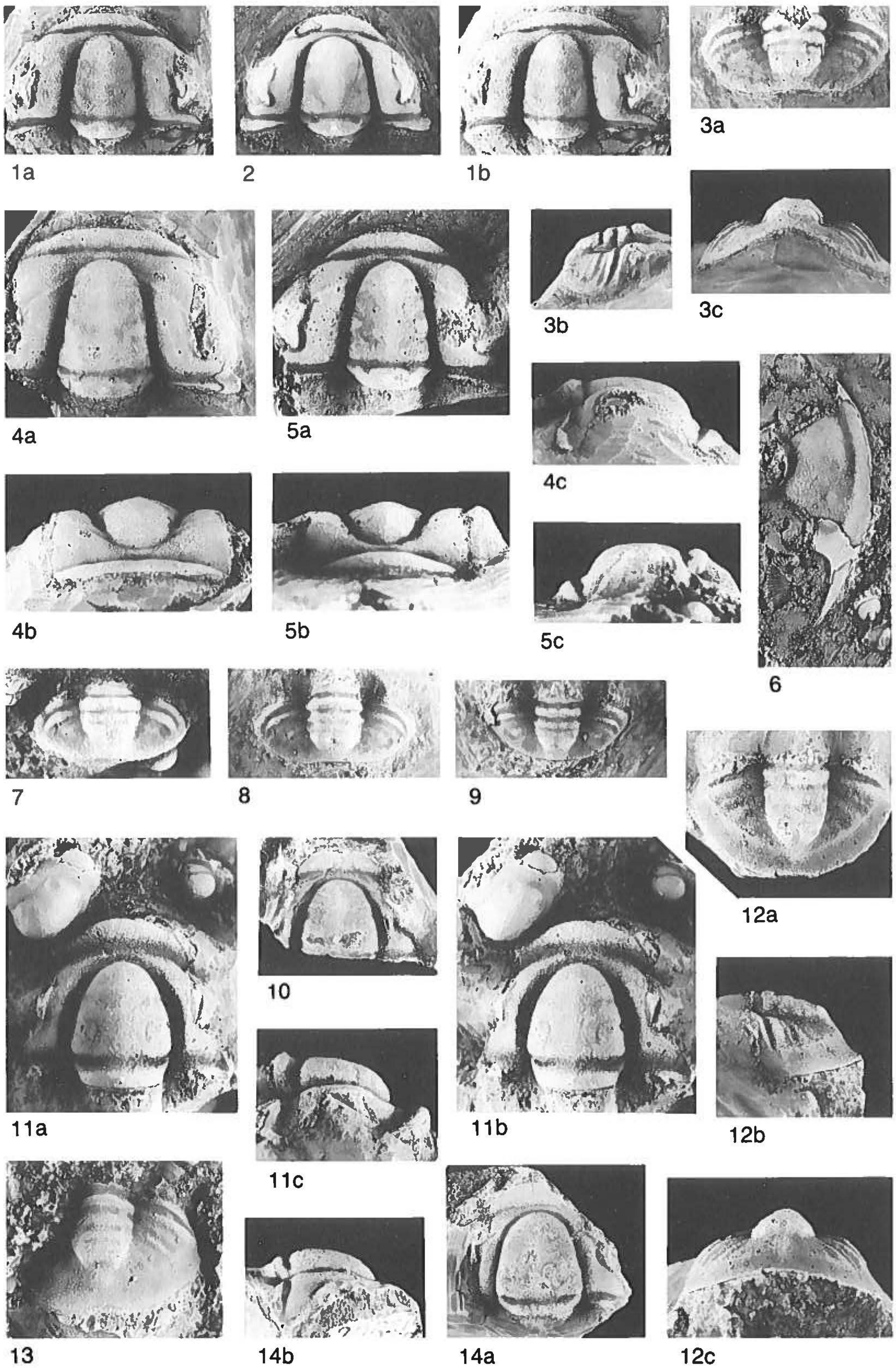
Material. – Four cranidia and four pygidia in GGU 225547, 225552, 225561, and 225564.

Diagnosis. – Cranidium typical of the genus. Pygidium broad, having two weak axial rings and long terminal piece; border wide, moderately downsloping, with concave surface; posterior margin having broad, very low, vertical arch.

Description. – Cranidium ranging in observed length from 6 to 9 mm. During holaspid ontogeny, lateral axial and anterior border furrows change from deep and wide to shallow and narrow; anterior border becomes wider (sag.), less convex, and together with palpebral area of fixigena changes from slightly upsloping to slightly downsloping. Glabella moderately convex, unfurrowed but may show weak muscle scars, tapered and narrowly rounded at front. Occipital ring simple, may have weak median node. Frontal area unequally divided, border being 2.0 to 2.5 times wider (sag.) than preglabellar field. Palpebral area of fixigena narrow. Anterior facial sutures subparallel.

Pygidium ranging in observed length from 4 to 7 mm, width from 8 to 10 mm. Axis broad, convex, tapering mainly at bluntly to broadly rounded rear, which has median indentation between pair of low bulges; length 0.75 to 0.80 that of pygidium; containing two weak rings on anterior half; postaxial ridge weak, continuing to posterior pygidial margin. Pleural field slightly convex, slightly downsloping; having 2 or 3 sets of weak furrows. Border wide, moderately downsloping, with smooth, concave surface. Posterior margin having broad, very low, vertical arch; spines lacking.

Remarks. – The cranidium of *S. catatate* differs little from those of other species of *Syspacheilus.* The pygidium, however, is intermediate in relative length between those of *S. dunoirensis* (Miller 1936, cf. Lochman & Hu 1961: pl. 26: 1, 2, 13, 18) and *S.* cf. *S. occidens* Lochman 1950 (cf. Lochman 1950: pl. 50: 27–29). The pygidium of *S. catatate* also is characterized by the broad, low, median arch of its posterior margin.


1a
2
1b
3a
4a
5a
3b
3c
4c
4b
5b
5c
6
7
8
9
12a
10
11a
11b
12b
11c
13
14b
14a
12c

Occurrence. – *S. catatate* is rare in lime grainstone from the lower 111 m of the Holm Dal Formation.

Family Menomoniidae Walcott

Genus *Bolaspidella* Resser 1937

Bolaspidella – Resser 1937: 3; Robison 1964: 552–554 (for other synonymy to date); Robison 1971: 801; Shaw 1966a: 292; Palmer 1968: B66; Öpik 1967: 367; Öpik 1970: 44; Shah & Sudan 1982: 237
Hysteropleura – Raymond 1937: 1094; Shaw 1966a: 290

Type species. – *Ptychoparia housensis* Walcott 1886, p. 201, pl. 25, fig. 5.

Remarks. – The concept and species content of *Bolaspidella* were previously reviewed (Robison 1964, 1971). That generic concept is followed here.

Shaw (1952) suggested that *Hysteropleura* is a synonym of *Bolaspidella,* but subsequently (1966a) resurrected the genus. In the latter paper, Shaw differentiated *Hysteropleura* by its lack of surface granulation, a narrower (tr.) anterior border on the cranidium, and smaller palpebral lobes. Of those characters, the lack of surface granulation on his illustrated specimens appears to be the result of poor preservation as internal molds. Moreover, on specimens that Shaw (1966a: pl. 34) assigned to *Hysteropleura* and *Bolaspidella,* the surfaces show no appreciable difference. On his illustrated specimens of *Hysteropleura* the anterior cranidial borders appear to be laterally covered by matrix, and the reduced transverse width may be only apparent rather than real. Also, some specimens that he assigned to *Hysteropleura* probably have longer palpebral lobes than those he assigned to *Bolaspidella* (cf. Shaw 1966a: pl. 34:4, 26). For these reasons, I continue to regard *Hysteropleura* as a junior synonym of *Bolaspidella.*

With little discussion, Öpik (1967: 367; 1970: 44) reassigned *Bolaspidella* to the Nepeidae. In my opinion, total morphology, biogeography, and biostratigraphy better support retention of *Bolaspidella* in the Menomoniidae. Supporting evidence is being assembled for separate publication.

Three new species of *Bolaspidella* were recently described by Shah & Sudan (1982) from Kashmir. The morphology and affinities of the specimens are difficult to evaluate because of poor preservation, but they do not seem to represent *Bolaspidella* (see also Jell 1986: 487). Among important differences, the specimens from Kashmir have a more tumid anterior cranidial border, a relatively larger glabella, and a more robust occipital ring. They also appear to differ in details of the lateral glabellar furrows.

Bolaspidella is common and widespread in Middle Cambrian open-shelf lithofacies of North America and Greenland. It also is present in Argentina (Poulsen 1960). The genus has an observed stratigraphic range from the *Ptychagnostus gibbus* to *Lejopyge laevigata* zones.

Bolaspidella stymacantha n. sp.

Fig. 22.2–4

Holotype. – Cranidium (Fig. 22.3), MGUH 17.315 from GGU 225540.

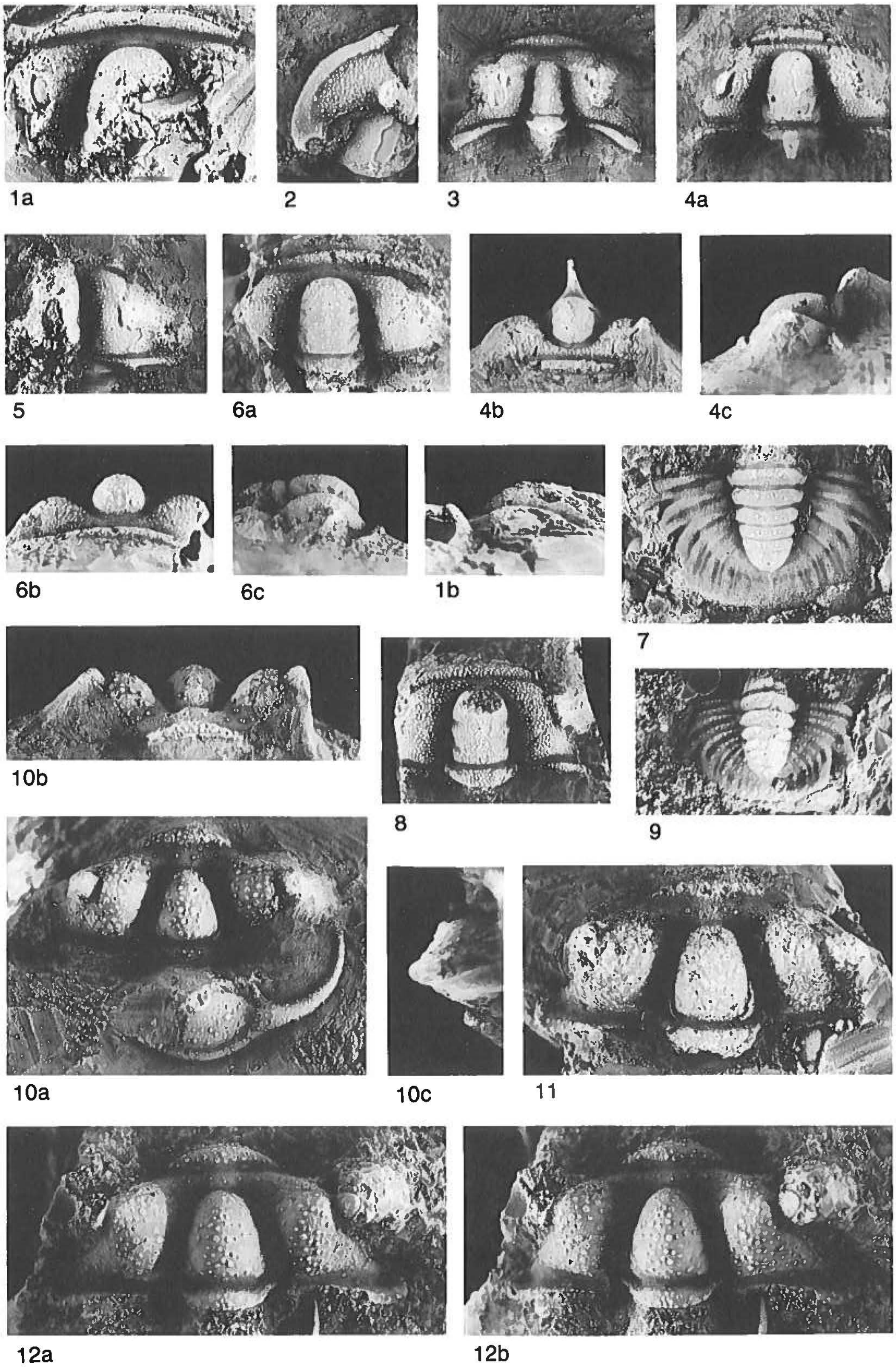
Material. – Fourteen cranidia and one librigena in GGU 225528, 225539, 225540, 225547, 225552, 225561, 225564, and 271414.

Diagnosis. – *Bolaspidella* having an erect occipital spine, moderately tapered glabella, palpebral lobe anterior from glabellar midpoint, and subequally divided frontal area.

Description. – Small *Bolaspidella* with narrow-based spine rising steeply from occipital ring, then distally curving backwards. Glabella moderately tapered, bluntly rounded at front; two pairs lateral furrows weakly developed. Frontal area subequally divided by border furrow. Palpebral lobe slightly anterior from glabellar midpoint. Anterior sections of facial suture subparallel to slightly convergent; posterior sections strongly divergent, sinuous. During holaspid ontogeny glabella decreases rather markedly in relative size, anterior cranidial border increases in medial width, and

Fig. 21. *Modocia planata* n. sp. and *Syspacheilus catatate* n. sp.

1–9. *Modocia planata* n. sp. 1. Exfoliated cranidium in stereo (a, b) view, MGUH 17.294 from GGU 225561, X 2.75. 2. Testaceous cranidium, MGUH 17.295 from GGU 225535, X 4.4. 3. Pygidium in dorsal (a), right-lateral (b), and rear (c) views; MGUH 17.296 from GGU 225561, X 3.3. 4. Holotype cranidium, exfoliated, in dorsal (a), frontal (b), and right-lateral 9c) views; MGUH 17.297 from GGU 225561, X 2.2. 5. Exfoliated cranidium in dorsal (a), frontal (b), and laft-lateral (c) views; MGUH 17.298 from GGU 271414, X 4.4. 6. Right librigena, mostly exfoliated; MGUH 17.299 from GGU 225563, X 2.75. 7–9. Pygidia; MGUH 17.300–17.302 from GGU 225535, 225564, and 225564; X 6.6, 4.4, and 5.5, respectively.
10–14. *Syspacheilus catatate* n. sp. 10. Incomplete cranidium, MGUH 17.303 from GGU 225564, X 1.65. 11. Cranidium in stereo (a, b) and right-lateral (c) views, associated with cranidium of *Bynumia metisensis* and pygidium of *Kormagnostus seclusus;* MGUH 17.304 from GGU 225561, X 4.4. 12. Holotype pygidium, exfoliated, in dorsal (a), left-lateral (b), and rear (c) views; MGUH 17.305 from GGU 225564, X 3.3. 13. Latex cast of exfoliated pygidium, MGUH 17.306 from GGU 225552, X 4.4. 14. Large, incomplete cranidium in dorsal (a) and right-lateral (b) views; MGUH 17.307 from GGU 225547, X 1.1.


1a
2
3
4a
5
6a
4b
4c
6b
6c
1b
7
10b
8
9
10a
10c
11
12a
12b

posterior area of fixigena widens transversely. Librigena relatively wide near base of genal spine, lateral margin irregularly curved. External surface covered by granules of bimodal size.

Remarks. – Of previously described species of *Bolaspidella*, only *B. drumensis* Robison 1964, *B. housensis*, *B. macgerriglei* (Raymond 1937), and *B. schucherti* (Raymond 1937) have an occipital spine. *B. stymacantha* differs from *B. drumensis* and *B. housensis* by having a more tapered glabella and a more regularly curved librigena. It differs from *B. macgerriglei* and *B. schucherti*, which may be synonyms, by having a longer glabella and less robust occipital spine.

Occurrence. – *B. stymacantha* is rare in all collections and is preserved in a variety of lithologies in the lower 110 m of the Holm Dal Formation.

Genus *Tavsenia* n. gen.

Type species. – *Tavsenia ditrema* n. sp.

Diagnosis. – Cephalon opisthoparian, anterior sections of facial suture strongly convergent; genal spines long, curved. Deep, wide grooves separating highly vaulted axial and pleural regions. Glabella unfurrowed, moderately tapered forward. Frontal area steeply downsloping; preglabellar field and anterior border subequal in sagittal length. Palpebral lobe wide and highly elevated. Genal field of librigena steeply inclined. Cephalic surface coarsely granulose.

Description. – Cranidium about twice wider than long. Axial furrow exceptionally wide and deep laterally, shallow but distinct anteriorly. Glabella unfurrowed, moderately tapering forward, bluntly to strongly rounded anteriorly. Occipital furrow moderately wide and deep, nearly straight except for slight forward curvature at abaxial ends. Frontal area steeply downsloping; maximum length about one-fourth that of cranidium. Preglabellar field and anterior border subequal in sagittal length, each being moderately convex; border narrowing outward. Anterior border furrow moderately wide and deep, fairly straight. Palpebral area of fixigena about 1.5 times wider than adjacent glabella, convex, steeply upsloping. Palpebral lobe unusually wide, bounded by prominent palpebral furrow, outer edge elevated above fixigena. Eye ridge weak. Posterior area of fixigena wider than occipital ring; posterior border furrow sharply defined, progressively widening and shallowing abaxially. Preocular margin strongly convergent, straight; postocular margin strongly divergent, slightly sinuous. Maximum observed cranidial length 7.3 mm.

Librigena having stout, moderately curved genal spine; length of spine exceeding remainder of librigena. Course of outer librigenal margin changing direction in broad bend near base of spine. Lateral border furrow moderately deep, merging with short posterior border furrow via broader and shallower furrow across base of genal spine. In reconstruction, genal field steeply inclined.

Cephalic exoskeleton heavily calcified and relatively thick. Surface covered with coarse granules of uneven size.

Remarks. – *Tavsenia* is erected to include what appear to be highly evolved representatives of the family Menomoniidae. Although not closely resembling any described genus, general structure of the cephalic axis and frontal area support an assignment to that family. A combination of strongly convergent anterior sections of the facial suture, relatively broad and steeply upsloping fixigenae, and long genal spines easily differentiates *Tavsenia* from all other menomoniid genera.

Specimens of *Tavsenia* from Greenland appear to be congeneric with a single cranidium from late Middle Cambrian rocks of Alaska that Palmer (1968: B102-B103, pl. 6: 14) described as 'Genus and species undetermined 4.' The only notable difference is in the shape of the anterior glabella, with the Greenland specimens being strongly rounded and the Alaskan specimen being bluntly rounded. Although all are exfoliated, the Greenland specimens appear to have had a pair of large pits in the anterior border furrow. Whether or not such

Fig. 22. *Balderia aspera* n. gen n. sp., *Bolaspidella stymacantha* n. sp and *Tavsenia ditrema* n. gen n. sp.

1, 5–9. *Balderia aspera* n. gen. and n. sp. 1. Fragment of anterior, large cranidium showing slightly tapered glabella and strongly upturned anterior border, in dorsal (a) and left-lateral (b) views; MGUH 17.308 from GGU 225561, X 3.3. 5. Fragment of right-lateral cranidium showing fixigena with palpebral lobe, MGUH 17.309 from GGU 225535, X 3.3. 6. Incomplete cranidium in dorsal (a), frontal (b), and right-lateral (c) views; MGUH 17.310 from GGU 225547, X 5.5. 7. Holotype pygidium, latex cast; MGUH 17.311 from GGU 225552, X 3.3. 8. Small holaspid cranidium with damaged, parallel-sided glabella; MGUH 17.312 from GGU 271414, X 7.7. 9. Latex cast of small pygidium, MGUH 17.313 from GGU 225535, X 6.6.

2–4. *Bolaspidella stymacantha* n. sp. 2. Left librigena, MGUH 17.314 from GGU 225547, X 7.7. 3. Holotype cranidium, MGUH 17.315 from GGU 225540, X 6.6. 4. Smaller holaspid cranidium preserving erect occipital spine, and having relatively large glabella and narrow posterior fixigenae; in dorsal (a), frontal (b), and left-lateral (c) views; MGUH 17.316 from GGU 225564, X 7.7.

10–12. *Tavsenia ditrema* n. gen. and n. sp., all X 4.4. 10. Exfoliated cranidium in dorsal (a, upper), frontal (b), and left-lateral (c) views, and associated left librigena (a, lower); MGUH 17.317 (cranidium) and 17.318 (librigena) from GGU 225564. 11. Exfoliated cranidium, MGUH 17.319 from GGU 225563. 12. Holotype cranidium, exfoliated, in stereo (a, b) view, MGUH 17.320 from GGU 225552.

pits were present in the Alaskan specimen is unclear. Until more material is known, I assign the Greenland specimens to *Tavsenia ditrema* and the Alaskan specimen to *Tavsenia* sp.

Tavsenia may also be represented in a collection from the Levis Formation of Quebec, Canada. Rasetti (1963: 579, pl. 70: 34, 35) described some librigenae as *Bolaspidella,* species undetermined. Based on present knowledge, however, they appear to be as similar to representatives of *Tavsenia* as they are to those of *Bolaspidella.*

Tavsenia ditrema n. sp.

Fig. 22.10–12

Holotype. – Cranidium (Fig. 22.12a, b), MGUH 17.320 from GGU 225552.

Material. – Seven cranidia and one librigena in GGU 225529, 225552, 225561, 225563, and 225564.

Diagnosis. – *Tavsenia* having strongly rounded anterior glabella and pair of large pits in anterior border furrow of cranidium.

Remarks. – Only cephalic sclerites of *T. ditrema* are known. Because matrix strongly adheres to the coarsely granulose external surface, all prepared specimens are mostly exfoliated.

Occurrence. – Rare in lime grainstone from the basal part of the Holm Dal Formation.

Family Onchonotopsididae Shaw

Emended diagnosis. – Small, opisthoparian ptychoparioids. Glabella large, usually unfurrowed, commonly ovate or rarely subquadrate, moderately convex to exceptionally tumid. Genal region downsloping. Preglabellar field absent to moderately wide (sag.). Cephalic border may be well defined, narrow, and of fairly uniform width or anterior border furrow may be effaced. Palpebral lobes short, anterior from or opposite glabellar midpoint. Thorax with 10 segments. Pygidium of moderate size, semicircular, with few segments; axis slightly tapered, extending almost to posterior margin; border undifferentiated; margin entire.

Remarks. – As emended, the Onchonotopsididae includes *Cryptoderaspis* Rasetti 1946, *Matania* Rasetti 1946, *Onchonotopsis* Rasetti 1946, and questionably *Durinia* n. gen. Some of the more stable features characterizing the family are the large and usually ovate glabella, downsloping genal regions, and short palpebral lobes. Specimens of *Genevievella rizantans* Lochman in Lochman & Duncan 1944 (also Lochman & Hu 1962), from Montana and Wyoming seem to represent a new genus with possible onchonotopsidid affinities.

As originally defined, Rasetti (1946: 458) noted a possible relationship between *Matania* and *Onchonotopsis* but otherwise held their affinities to be obscure. Later, Shaw (1966b: 856) assigned both genera to a new family Onchonotopsididae, which he considered to "belong near the family Menomoniidae in the taxonomic scheme that is used in the Treatise on Invertebrate Paleontology." On the basis of shared cranidial features, I agree that *Matania* and *Onchonotopsis* should be united in the same family. All menomoniids, however, have a relatively small glabella, whereas *Matania* and *Onchonotopsis* have a large glabella. Shaw's suggestion of close onchonotopsidid and menomoniid affinity seems to have been strongly influenced by his assignment of a poorly preserved, incomplete trilobite having a minimum of 22 thoracic segments to *Onchonotopsis pergibba* Rasetti 1946. In my opinion, that specimen is generically indeterminate. Elongation of the glabella of *Onchonotopsis* is probably a paedomorphic character, which in most trilobites correlates with a reduction in the number of thoracic segments. Therefore, the many-segmented specimen illustrated by Shaw almost surely does not represent *Onchonotopsis,* and the number of thoracic segments in that genus remains to be verified. A complete specimen of *Matania quadrata* n. sp., which is described here, has only 10 thoracic segments. Because of basic differences in cranidial structure, especially structure of the glabella, I suggest that the phyletic affinity of onchonotopsidids and menomoniids is probably remote.

From available morphologic, biogeographic, and biostratigraphic evidence, it now appears likely that the Lonchocephalidae, Catillicephalidae, and Onchonotopsididae are closely related families. Rasetti (1954) has discussed phylogenetic aspects of the Lonchocephalidae and Catillicephalidae. The subrectangular glabella and characteristic lateral glabellar furrows in early holaspides of *Matania matuta* n. sp., especially the posterior pair of furrows that turns backward and almost isolates the basal lobes, are characters shared with the Lonchocephalidae and Catillicephalidae. The pygidium of *M. quadrata* is the first to be documented for the Onchonotopsididae, and it is in accord with the general size and form present in the Lonchocephalidae and Catillicephalidae.

Matania, with less derived glabellar features, appears to be the ancestral genus of the Onchonotopsididae. Although it likely descended from a lonchocephalid, the generic source remains unclear.

Representatives of the Onchonotopsididae are presently known from only open-shelf lithofacies of North America and Greenland. Their age is latest Middle Cambrian (*Lejopyge laevigata* Zone) and probably earliest Late Cambrian.

Genus *Cryptoderaspis* Rasetti 1946

Cryptoderaspis – Rasetti 1946: 451; Rasetti in Harrington et al. 1959: O517; Palmer in Palmer & Peel 1981: 35–36.

Type species. – *Cryptoderaspis metisensis* Rasetti 1946, pp. 451–452, pl. 68, figs 28–30.

Emended diagnosis. – Onchonotopsidids known from cranidium. Glabella ovate, highly tumid, posterior end overhanging occipital ring. Frontal area relatively long, convexly downsloping; border furrow effaced, leaving preglabellar field and anterior border undifferentiated. Ventral edge of anterior cranidium nearly flat, having no anterior arch. Palpebral lobe opposite anterior third of glabella. Anterior sections of facial suture subparallel. Occipital ring steeply downsloping.

Remarks. – Although *Cryptoderaspis* has not previously been assigned to a family, its ovate and unfurrowed glabella, downsloping genal regions, and short palpebral lobes leave little doubt that it should be united with other genera in the Onchonotopsididae. Nevertheless, it can be easily differentiated from other genera in the family by its wider and more steeply downsloping genal regions and effaced anterior border furrow. The steeply downsloping occipital ring is unusual, not only among onchonotopsidids, but among polymeroid trilobites in general.

Cryptoderaspis is a rare genus, known from Quebec, Canada, and North Greenland. Its age is latest Middle Cambrian (upper *Lejopyge laevigata* Zone) and probably earliest Late Cambrian.

Cryptoderaspis metisensis Rasetti 1946

Fig. 23.1–4

Cryptoderaspis metisensis – Rasetti 1946: 451–452, pl. 68: 28–30

Cryptoderaspis cf. *C. metisensis* Rasetti – Palmer in Palmer & Peel 1981: 36, pl. 6: 9, 12

New material. – Six cranidia in GGU 225528, 225535, 271403, and 271414.

Diagnosis. – Characters of the genus.

Remarks. – The new cranidia representing *Cryptoderaspis* all have an ovate glabella but glabellar outline varies in detail from subcircular to moderately tapered. Some (e.g. Fig. 23.4) closely resemble the types of *C. metisensis*. Without larger samples, significance of the variation can not be adequately evaluated. In the absence of other significant differences, all of the new specimens are provisionally assigned to *C. metisensis*.

Occurrence. – Rare in lime wackestone and grainstone from the basal 22 m of the Holm Dal Formation.

Genus *Durinia* n. gen.

Type species. – *Durinia granulosa* n. sp.

Diagnosis. – Onchonotopsidid having stout occipital spine. Glabella subrectangular to ovoid, strongly convex. Preglabellar field variably developed.

Description. – Onchonotopsidid known from cranidium; maximum observed length about 5 mm, exclusive of occipital spine. Axial furrow deep. Glabella large, subrectangular to ovoid in dorsal view, strongly convex, unfurrowed. Occipital furrow deep, bowed backwards. Occipital ring extending into broad-based, stout, moderately erect, median spine. Frontal area short; preglabellar field variably developed; anterior border narrow (sag.), broadly bowed forwards. Palpebral area of fixigena moderately convex, on average slightly downsloping. Palpebral lobe short, anterior from glabellar midpoint. Eye ridge weak, oblique. Posterior area of fixigena strongly downsloping. Anterior sections of facial suture parallel to slightly convergent.

Remarks. – *Durinia* is tentatively assigned to the Onchonotopsididae on the basis of its relatively large glabella, downsloping genal regions, and short palpebral lobes. It differs from all other genera in the family by the presence of an occipital spine.

Two species are presently included in *Durina*. The type species, *D. granulosa*, is here described from the Holm Dal Formation. The other species, *Onchonotopsis? spinicollis* Rasetti 1963, from Quebec, is here reassigned to *Durinia*.

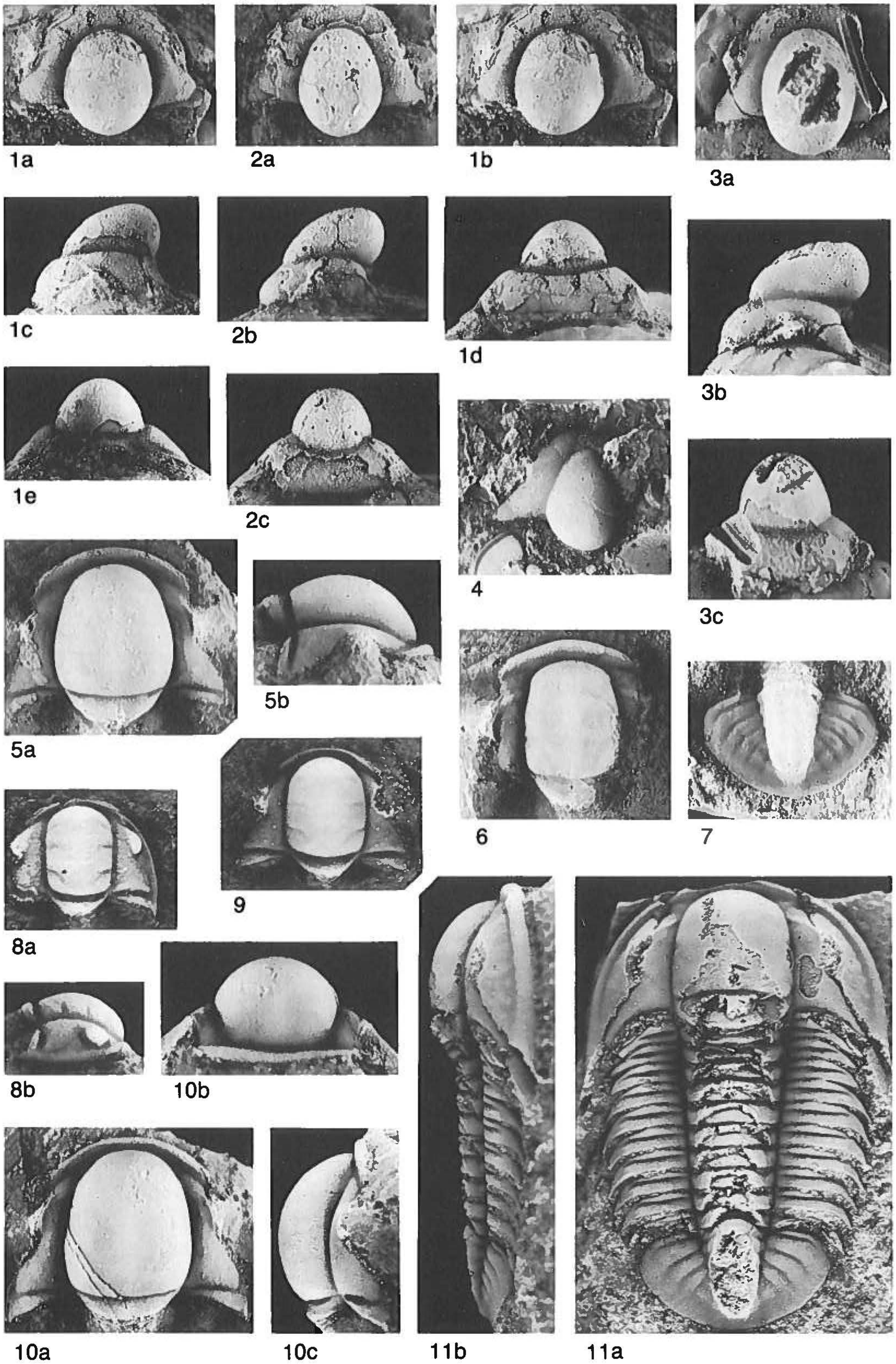
In Greenland, *D. granulosa* is associated with a fauna of the *Lejopyge laevigata* Zone. In Quebec, *D. spinicollis* is known from a single conglomeratic boulder of the Lévis Formation, and the only other reported trilobite in the boulder is *Athabaskiella longicauda* (Rasetti 1963, table 2), which also is present in the middle of the Holm Dal Formation in Freuchen Land, North Greenland.

Durinia granulosa n. sp.

Figs 24.1–5, 25.1

Holotype. – Cranidium (Fig. 24.1a-c), MGUH 17.332 from GGU 225535.

Material. – More than 20 cranidia in GGU 225528, 225535, 225561, and 271414.


1a
2a
1b
3a
1c
2b
1d
3b
1e
2c
4
3c
5b
5a
6
7
9
8a
8b
10b
10a
10c
11b
11a

Diagnosis. – *Durinia* of small size; largest observed cranidium about 3 mm long, exclusive of occipital spine, but most cranidia are less than 2 mm long. Glabella subrectangular in smaller specimens, becoming ovoid in largest specimens. Preglabellar field absent or barely developed. Palpebral area of fixigena about half as wide as adjacent glabella. Exoskeleton moderately thick; dorsal surface covered with abundant, rather coarse granules.

Remarks. – *D. granulosa* differs from *D. spinicollis* by having a coarsely granular rather than a smooth test, possibly representing different physiological adaptation. The character, however, should be used with care; specimens of *D. granulosa* are commonly exfoliated and the internal mold may be smooth (e.g. Fig. 25.1). On average, specimens of *D. granulosa* are about half the size of those of *D. spinicollis*. Also, they usually have a subrectangular rather than an ovoid glabella, a shorter preglabellar field, wider fixigenae, and more anterior eyes. All of the latter differences probably should be accorded little taxonomic value because similar differences commonly develop during the ontogeny of ptychoparioid trilobites.

Of trilobites in the Holm Dal Formation, *D. granulosa* superficially resembles and may be confused with *Glaphyraspis alpha*. Among the distinguishing characters of *D. granulosa* are a more convex glabella that lacks lateral furrows, a concave rather than a convex preglabellar field, more downsloping fixigenae, and larger and more numerous granules on the dorsal surface.

Occurrence. – *D. granulosa* is rare to moderately common in lime grainstone and wackestone from the lower 22 m of the Holm Dal Formation.

Genus *Matania* Rasetti 1946

Matania – Rasetti 1946: 458; Rasetti in Harrington et al. 1959: O519

Type species. – *Matania ovata* Rasetti 1946, p. 458, pl. 70, figs 11–14.

Emended diagnosis. – Onchonotopsidids lacking preglabellar field. Glabella subquadrate to ovate, moderately to strongly convex. Ventral edge of anterior cranidium nearly flat, having no anterior arch. Anterior sections of facial suture approximately parallel. Palpebral lobe opposite glabellar midpoint in mature holaspides. Occipital ring simple, medially widened, with strongly rounded posterior margin. Librigena having narrow lateral border and genal spine of moderate length.

Thorax containing 10 segments. Pleural tips moderately falcate.

Pygidium semicircular. Axis slightly tapered, extending almost to posterior margin; ring furrows mostly effaced. Pleural field slightly wider than axis; convex mesially, becoming concave marginally. Four pairs of pleural furrows clearly evident adaxially, disappearing in marginal area; interpleural furrows undeveloped. Border undifferentiated. Margin entire.

Remarks. – *Matania* presently includes *M. ovata* and two new species, *M. matuta* and *M. quadrata*. Representatives of *Matania* are known from Quebec, Canada, and North Greenland. Although the first-described specimens were assigned an early Late Cambrian age (Rasetti 1946), current biostratigraphic evaluation indicates that *Matania* is not known with certainty to range beyond the *Lejopyge laevigata* Zone of late Middle Cambrian age.

Fig. 23. *Cryptoderaspis metisensis* Rasetti, *Matania matuta* n. sp. and *Matania quadrata* n. sp.

1–4. *Cryptoderaspis metisensis* Rasetti. 1. Cranidium with subcircular glabella, in stereo (a, b), left-lateral (c), frontal (d), and rear (e) views; MGUH 17.321 from GGU 225528, X 5.5. 2. Cranidium with typical ovate glabella, in dorsal (a), left-lateral (b), and frontal (c) views; MGUH 17.322 from GGU 225528, X 6.6. 3. Damaged cranidium in dorsal (a), left-lateral (b), and frontal (c) views; MGUH 17.323 from GGU 271414, X 6.6. 4. Latex cast of cranidium with moderately tapered glabella, MGUH 17.324 from GGU 225535, X 6.6.

5, 8–10. *Matania matuta* n. sp., all from GGU 225535. 5. Intermediate holaspid cranidium with ovate glabella, in dorsal (a) and right-lateral (b) views; MGUH 17.325, X 8.8. 8. Early holaspid(?) cephalon with subrectangular glabella and weakly developed lateral glabellar furrows, in dorsal (a) and right-lateral (b) views; MGUH 17.326, X 13.2. 9. Early holaspid cranidium with nearly effaced lateral glabellar furrows, MGUH 17.327, X 11. 10. Holotype, large holaspid cranidium in dorsal (a), frontal (b), and right-lateral (c) views; MGUH 17.328, X 7.7.

6, 7, 11. *Matania quadrata* n. sp., all from GGU 271408. 6. Small holaspid cranidium, MGUH 17.329, X 13.2. 7. Latex cast of pygidium, MGUH 17.330, X 5.5. 11. Holotype exoskeleton in dorsal (a) and right-lateral (b) views, MGUH 17.331, X 5.5.

Matania matuta n. sp.

Fig. 23.5, 8–10

Holotype. – Cranidium (Fig. 23.10a-c), MGUH 17.328 from GGU 225535.

Material. – About 20 cranidia and one cephalon, the latter probably an early holaspid; all in GGU 225535.

Description. – Glabella large and moderately convex; subrectangular in early holaspides, becoming ovate in middle and late holaspides. Lateral glabellar furrows weakly developed in early holaspides, effaced in middle and late holaspides; S1 oblique backwards and convex, S2 transverse. Palpebral lobe anterior from glabellar midpoint in early holaspides, shifting opposite glabellar midpoint in middle and late holaspides. Anterior border furrow strongly curved forward. Eye ridge weak, strongly oblique. Librigena known from single, probably early holaspid; transversely narrow with short genal spine.

Remarks. – Cranidia of *M. matuta* most closely resemble those of *M. ovata*, but are less tumid in the posterior glabella. When viewed from the side, the posterior glabella of *M. ovata* rises abruptly from the occipital furrow, forming a steplike dislocation in the dorsal profile at the occipital furrow (Rasetti 1946, pl. 70: 12, 14). In comparison, the profile of *M. matuta* has an indentation at the occipital furrow but no steplike dislocation (Fig. 23.5b, 10c).

Occurrence. – Specimens are preserved in lime grainstone and packstone from about 22 m above the base of the Holm Dal Formation.

Matania quadrata n. sp.

Fig. 23.6, 7, 11

Holotype. – Complete specimen (Fig. 23.11a, b), MGUH 17.331 from GGU 271408.

Material. – One complete dorsal exoskeleton, 3 cranidia, and 4 pygidia in GGU 271408.

Description. – Glabella subquadrate. Anterior border furrow slightly curved forward. Eye ridge weak, slightly oblique. Characters of librigena, thorax, and pygidium as described for genus.

Remarks. – *M. quadrata* differs from *M. ovata* and *M. matuta* in having a subquadrate rather than an ovoid glabella, the anterior border furrow of the cranidium is less curved, and the eye ridge is less oblique. The anterior border and eye ridge are well separated in *M. quadrata* but anteriorly are close together in *M. matuta*.

The holotype of *M. quadrata* is the first complete specimen that can be assigned to the Onchonotopsididae without question. Also the pygidium of this species is the first known for the family.

Occurrence. – Preserved in dark lime mudstone from about 16 m above the base of the Holm Dal Formation.

Genus *Onchonotopsis* Rasetti 1946

Onchonotopsis – Rasetti 1946: 460; Rasetti in Harrington et al. 1959: O519; Shaw 1966b: 856; Palmer 1968: B91-B92

Type species. – *Onchonotopsis pergibba* Rasetti 1946, p. 460, pl. 70, figs 23–26.

Emended diagnosis. – Onchonotopsidids known from only cranidium. Glabella exceptionally tumid, slightly overhanging occipital furrow. Preglabellar field short, sagittal length ranging from subequal to approximately twice that of anterior border. Anterior border gently bowed forward, anterior arch moderate. Palpebral area of fixigena transversely narrow, palpebral lobe anterior from glabellar midpoint. Occipital ring usually simple, short, and moderately bowed backwards; rarely bearing median spine.

Remarks. – Although representatives overlap in observed stratigraphic range, *Onchonotopsis* apparently was derived from *Matania*. Major differences are the extreme glabellar inflation and development of an anterior arch in *Onchonotopsis* (e.g. Fig. 24.6d, 10c, 11d, 12c). The latter feature may be related to a functional adaptation for burrowing (see Eldredge 1970: 12–15).

Lazarenko (in Lazarenko & Nikiforov 1968: 64–65, pl. 8: 15–17) assigned specimens from the Upper Cambrian of the Siberian platform to a new species, *Onchonotopsis cara*. These, however, appear to be homeomorphs of representatives of *Onchonotopsis* from North America and Greenland. Among other differences, the Siberian specimens have a more angular glabellar outline, upsloping palpebral areas of the fixigenae, and significantly larger palpebral lobes. They probably should be assigned to a new genus.

Also from the Upper Cambrian of the Siberian platform, Lazarenko & Datsenko (1967: 24, table 1) mentioned and listed *Onchonotopsis timios*. An apparent lack of description and illustration, in accord with the International Code of Zoological Nomenclature, renders that name a *nomen nudum*.

Onchonotopsis currently includes *O. eminens* (Raymond 1937), *O. occidentalis* Palmer 1968, *O. pergibba* Rasetti 1946, *O. spinicollis* Rasetti 1963, and a new species *O. physala*. Except for *O. spinicollis*, all species lack an occipital spine.

Representatives of *Onchonotopsis* are known from open-shelf lithofacies of Canada (Quebec), the United States (Alaska, Vermont), and North Greenland. Although the stratigraphic relationships of some specimens are unclear, none are known with certainty to occur in rocks other than those of the *Lejopyge laevigata* Zone (Robison 1984) of late Middle Cambrian age.

Onchonotopsis pergibba Rasetti 1946

Fig. 24.9–12

Onchonotopsis pergibba – Rasetti 1946: 460, pl. 70: 23–26

Onchonotopsis pergibba – Shaw 1966b: 856, pl. 99: ?12 (not 13)

New material. – Ten cranidia in GGU 225528, 225529, 225535, 225537, 225561, 225563, and 271403.

Diagnosis. – *Onchonotopsis* having short preglabellar field, subequal in sagittal length with that of anterior border. Glabella very gibbose. Anterior facial sutures approximately parallel. Eye ridge absent or very weak. Occipital ring nonspinose.

Remarks. – *O. pergibba* is a small trilobite. Cranidia from both Quebec and North Greenland range up to only about 3 mm in observed length. The swollen glabella is moderately variable in dorsal outline as well as in lateral profile.

O. pergibba seems to be closely similar to *O. eminens* in size and general features, but *O. eminens* has been illustrated only by line drawings. I suggest that comparison of type specimens may show enough similarity to justify synonymy of the two species.

For reasons mentioned in the foregoing family discussion, Shaw's (1966b) specimen with a many-segmented thorax is excluded from *Onchonotopsis*. An associated cranidium appears to be too poorly preserved to warrant assignment to a species.

Occurrence. – All new specimens are preserved in lime grainstone from the lower 22 m of the Holm Dal Formation.

Onchonotopsis physala n. sp.

Fig. 24.6–8

Holotype. – Cranidium (Fig. 24.6a-d), MGUH 17.337 from GGU 225561.

Material. – Five cranidia in GGU 225528, 225561, 271414, and 271417.

Description. – Relatively large representatives of *Onchonotopsis*, cranidia ranging up to about 7 mm in observed length. Preglabellar field relatively long, sagittal length being about twice that of anterior border. Glabella extraordinarily tumid. Anterior facial suture slightly divergent. Eye ridge not evident. Occipital ring nonspinose.

Remarks. – Representatives of *O. physala* resemble those of *O. occidentalis* in relative length of the preglabellar field and slight divergence of the anterior facial sutures. The glabella, however, is much more highly inflated in *O. physala*, and the anterior border is sagittally wider in *O. occidentalis*. Associated index fossils indicate that *O. occidentalis* is from the lower part of the *Lejopyge laevigata* Zone whereas *O. physala* is from the upper part of the same zone. Therefore, stratigraphic position supports the possibility that *O. physala* evolved from *O. occidentalis* by increase in glabellar tumescence and decrease in border width.

Representatives of *O. physala* also rather closely resemble those of *O. pergibba*. The largest observed cranidia of *O. physala* are more than twice as long as those of *O. pergibba*. Nevertheless, cranidia of the same size (cf. Fig. 24.6, 10) can readily be distinguished by the distinctly longer preglabellar field, slightly divergent anterior facial sutures, and more tumid glabella of *O. physala*. Both cranidial forms are associated in at least one collection (GGU 225528), and it is conceivable that they represent sexual dimorphs of one species. However, I provisionally assign the two forms to separate species because cranidia of only one form are present in at least six other collections.

Although *O. physala* and *O. spinicollis* both show a relative elongation of the preglabellar field, *O. spinicollis* differs from all species of *Onchonotopsis* by the presence of a large occipital spine. In addition, it has a weak anterior border furrow.

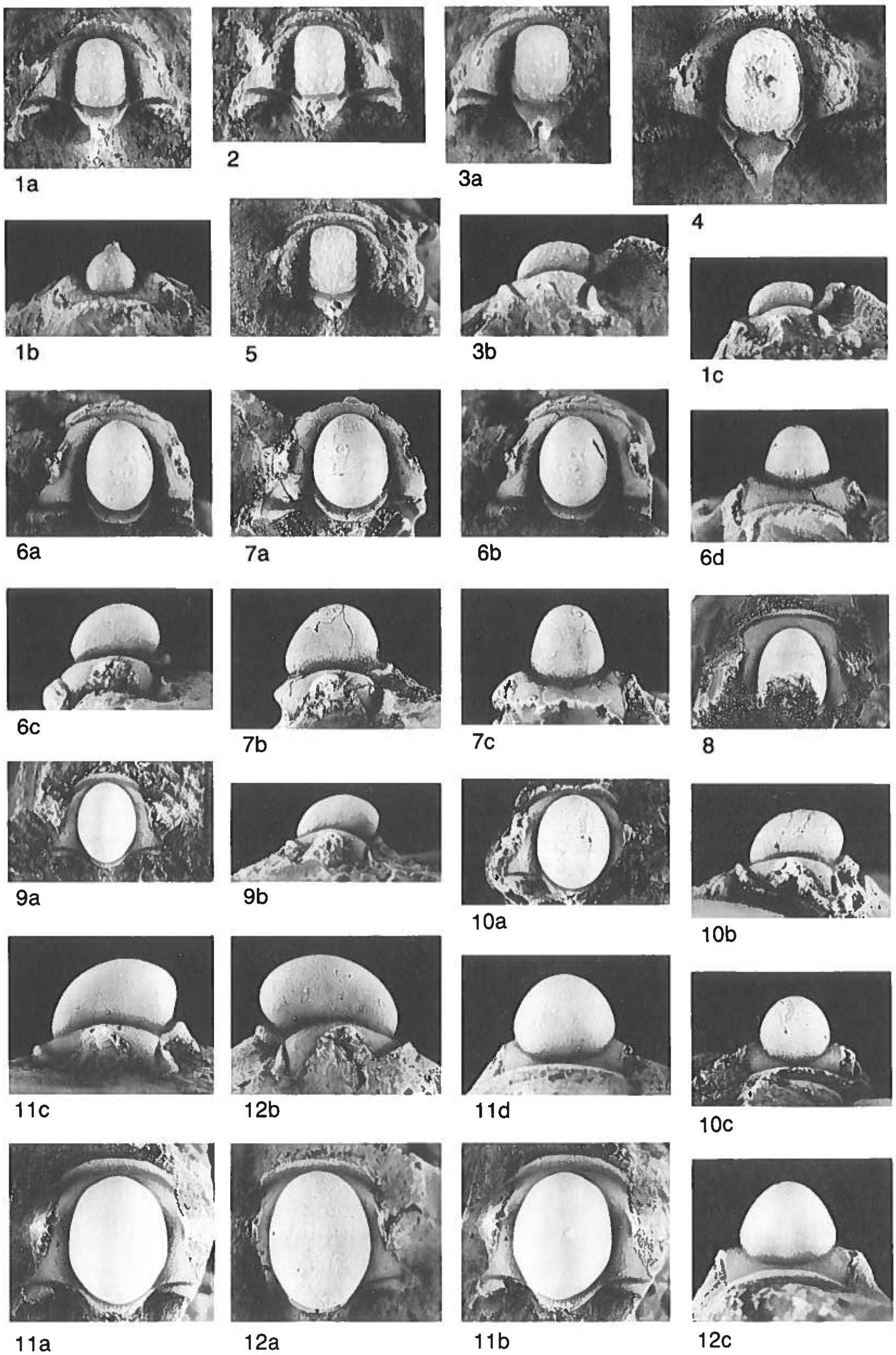
Occurrence. – The species is very rare in lime packstone and grainstone from the lower 93 m of the Holm Dal Formation.

?Family Solenopleuridae Angelin

Genus *Balderia* n. gen.

Type species. – *Balderia aspera* n. sp.

Diagnosis. – Cranidium of solenopleurid aspect. Pygidium characterized by deep clefts in anterolateral margins forming two pairs of robust, blunt spines. Pygidial axis tapered, having 5 or 6 rings. Dorsal surface of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cranidium covered with dense granules of bimodal size, pygidium having scattered granules of variable size.

Description. – Cranidium about two-thirds wider than long. Axial furrow broad, deep. Glabella moderately convex; subparallel sided to slightly tapered, bluntly rounded anteriorly; lateral furrows undeveloped, but surface areas corresponding to S1 and S2 lack granules. Occipital furrow narrow, shallow; straight or slightly bowed backwards. Occipital ring wider than back of glabella, lacking medial node or spine. Frontal area short, subequally divided by narrow, nearly straight border furrow; preglabellar field downsloping; anterior border sagitally narrow, transversely wide, becoming strongly upturned during holaspid ontogeny. Eye ridge weak, transverse. Palpebral area of fixigena slightly narrower than adjacent glabella, moderately convex, on average slightly downsloping. Palpebral lobe short, anterior of glabellar midpoint. Posterior area of fixigena similar to occipital ring in transverse width. Anterior sections of facial suture changing from parallel to slightly divergent during holaspid ontogeny. Dorsal surface having dense granules of bimodal size, except in furrows and at positions of undeveloped S1 and S2.

Pygidium semicircular, width about twice length. Axis moderately tapered, strongly rounded at posterior end; length about three-fourths that of entire pygidium; containing 5 or 6 rings and terminal piece. Pleural region slightly convex adaxially, passing into slightly concave marginal area. Anterior pleural region having two deep clefts, isolating two robust, bluntly terminated spines that do not extend beyond disrupted pygidial margin. Pleural furrows prominent on anteriormost three pleurae; followed rearward by 1 to 3 sets of pleural and interpleural furrows of subequal depth, all disappearing near outer pygidial margin. Inner margin of wide pseudoborder marked by slight deepening of pleural and interpleural furrows, probably above inner margin of doublure. Dorsal surface having scattered granules of variable size; largest granules occurring in pairs, one pair on crest of each axial ring.

Remarks. – The cranidium of *Balderia* has a solenopleurid aspect, but the pygidium seems to be unique, at least among Cambrian trilobites, in having marginal spines formed from deep clefts in the anterolateral pleural regions rather than as projections from the pygidial margin. To my knowledge, overall characters of neither the cranidium nor the pygidium closely match those of any described trilobite genus. On the basis of cranidial characters, *Balderia* is questionably assigned to the Solenopleuridae. Otherwise, its phyletic affinities are unclear.

Balderia aspera n. sp.

Fig. 22.1, 5–9

Holotype. – Pygidium (Fig. 22.7), MGUH 17.311 from GGU 225552.

Material. – Four cranidia and 2 pygidia in GGU 225535, 225547, 225552, 225561 and 271414.

Description. – Characters of genus.

Remarks. – Large holaspid cranidia of *B. aspera* are known only from fragments, but these are sufficient to determine important taxonomic characters. During holaspid ontogeny, lateral sides of the glabella changed from near parallel to slightly tapered, the anterior cranidial border changed from slightly downsloping to strongly upturned, eyes migrated slightly toward the posterior, and spacing between large granules on the cranidial surface became wider. Lack of surface granules at the S1 and S2 positions gives the glabella the appearance of having weak lateral furrows, but actually they are not developed. The occipital ring is unusual in being distinctly wider in transverse direction than the adjacent glabella.

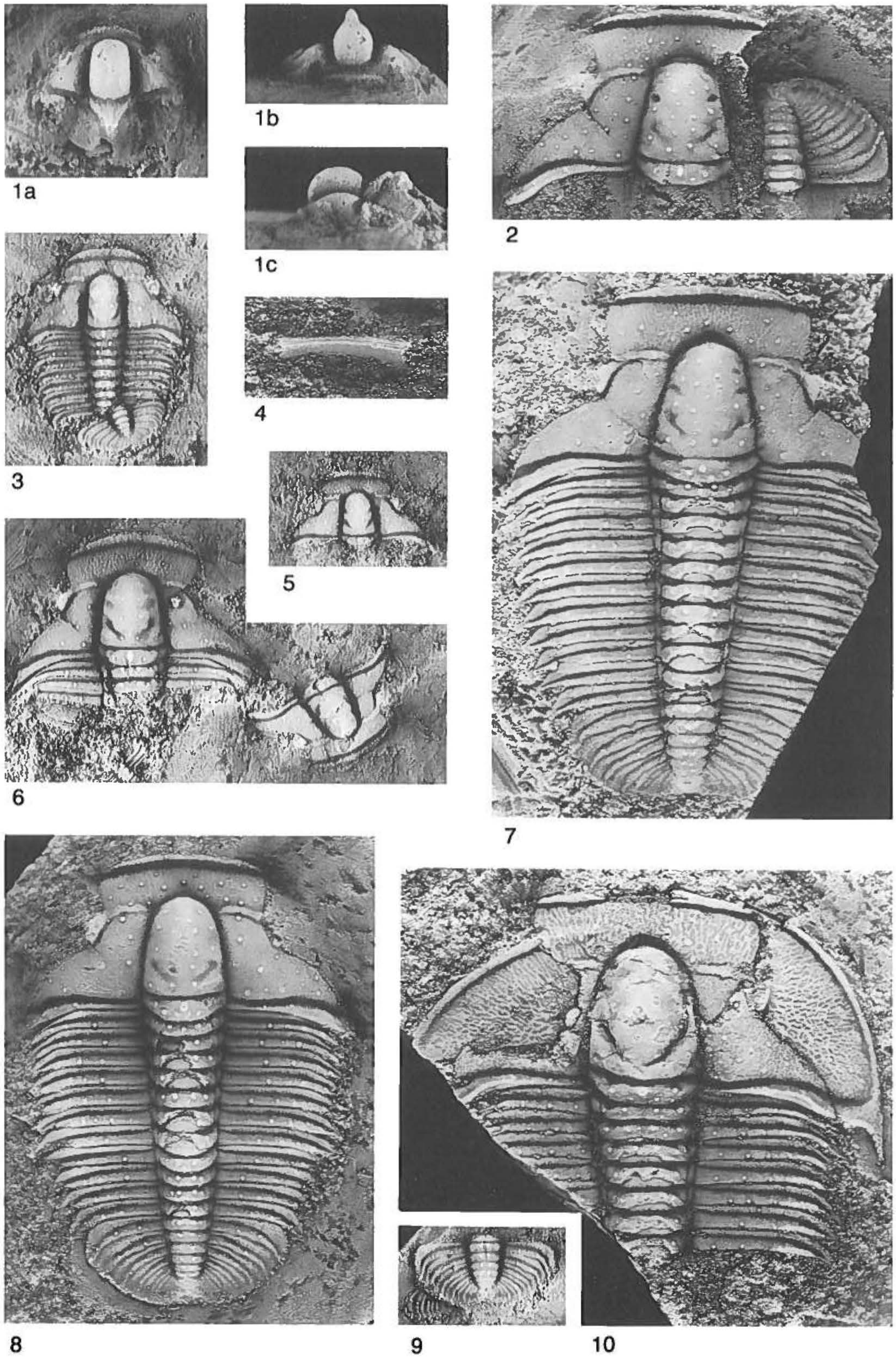
Occurrence. – *B. aspera* is rare in lime packstone and grainstone from the lower 111 m of the Holm Dal Formation.

Fig. 24. *Durinia granulosa* n. gen. n. sp., *Onchonotopsis physala* n. sp. and *Onchonotopsis pergibba* Rasetti.

1–5. *Durinia granulosa* n. gen. and n. sp., all X 8.8. 1. Holotype cranidium in dorsal (a), frontal (b), and left-lateral (c) views; MGUH 17.332 from GGU 225535. 2, 3, 5. Cranidia, each with typical subrectangular glabella, in dorsal (2, 3a, 5) and left-lateral (3b) views; MGUH 17.333–17.335, all from GGU 225535. 4. Large, mostly exfoliated cranidium with ovoid glabella; MGUH 17.336 from GGU 225561.

6–8. *Onchonotopsis physala* n. sp. 6. Holotype, small, exfoliated cranidium in stereo (a, b), left-lateral (c), and frontal (d) views; MGUH 17.337 from GGU 225561, X 8.8. 7. Large exfoliated cranidium, anterior border broken off, in dorsal (a), left-lateral (b), and frontal (c) views; MGUH 17.338 from GGU 225528, X 3.3. 8. Large, incomplete cranidium showing anterior border; MGUH 17.339 from GGU 271417, X 3.3.

9–12. *Onchonotopsis pergibba* Rasetti, all X 8.8. 9. Small cranidium in dorsal (a) and left-lateral (b) views, MGUH 17.340 from GGU 225535. 10. Intermediate cranidium in dorsal (a), left-lateral (b), and frontal (c) views; MGUH 17.341 from GGU 225528. 11. Large cranidium in stereo (a, b), left-lateral (c), and frontal (d) views; MGUH 17.342 from GGU 225535. 12. Large cranidium in dorsal (a), right-lateral (b), and frontal (c) views; MGUH 17.343 from GGU 225563.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Family uncertain

Genus *Conopolus* n. gen.

Type species. – *Conopolus granulus* n. sp.

Diagnosis. – Glabella large, conical. Anterior cranidial border narrow (sag.), fairly straight; preglabellar field barely developed. Palpebral area of fixigena moderately wide, downsloping; palpebral lobe just anterior of glabellar midpoint. Anterior sections of facial suture parallel. Pygidium semicircular with short, tapered axis of 3 or 4 rings. Pleural field having 3 or 4 sets of radial, pleural and interpleural furrows of near uniform depth. Pygidial margin smooth except for pair of very short anterolateral spines.

Description. – Cranidium about twice wider than long. Axial furrow narrow, shallow. Glabella large, conical. Occipital furrow narrow, slightly curved backward. Occipital ring short. Frontal area very short; preglabellar field barely developed; anterior border narrow (sag.), convex, fairly straight, having low dorsal arch. Palpebral area of fixigena moderately downsloping, eye ridge weak, palpebral lobe anterior from glabellar midpoint. Posterior area of fixigena about two-thirds width of occipital ring. Anterior sections of facial suture parallel, straight; posterior sections divergent, convex.

Pygidium semicircular, width about twice length. Axis moderately tapered, length 0.5 to 0.6 times that of pygidium; containing 3 or 4 rings and tiny terminal piece. Pleural field gently convex, on average downsloping; marked by 3 or 4 sets of radial, mostly parallel, distally converging, pleural and interpleural furrows of near-uniform depth. Anterior interpleural furrow reaching lateral margin, other furrows of pleural field terminating just short of outer margin. Anterior segment terminating in very short anterolateral spine, remaining pygidial margin smooth.

Remarks. – Cranidia in several collections from the Holm Dal Formation closely resemble two previously illustrated cranidia, one from Texas and one from Quebec. A small fragmentary cranidium from west Texas was described and figured as *Blountiella* sp. undet. by Wilson (1954: 267, pl. 24: 16), but I do not consider it to be congeneric with *Blountia? alemon* Walcott 1916b, the type species of *Blountiella* Resser 1938. The Texas cranidium was reported by Wilson to be associated with a *Cedaria* Zone fauna in a limestone boulder that was collected from the Woods Hollow Formation of Middle Ordovician age. A well-preserved cranidium from Quebec was described and figured as 'Undetermined cranidium No. 1' by Rasetti (1963: 593, pl. 70: 26–28), who concluded that although it could not be referred to any described genus, it did not seem proper to propose a new one based on a single specimen. Together, the Texas and Quebec cranidia and material from North Greenland here provide the basis for description of the new genus *Conopolus*. Although sharing several distinctive characters, the known specimens of *Conopolus* also show sufficient trivial differences to warrant their assignment to two new species, *C. granulus* from North Greenland and Texas, and *C. rasettii* from Quebec.

Conopolus is a ptychoparioid trilobite of otherwise unknown phyletic affinity. The large, conical glabella together with the narrow, nearly straight anterior cranidial border and barely developed preglabellar field are characteristic.

In the absence of complete specimens, associated pygidia from North Greenland, with radial sets of pleural and interpleural furrows, are assigned to *Conopolus* with question. Although resembling rare, unassigned pygidia from the *Elvinia* Zone of Pennsylvania (Wilson 1951: 650, pl. 95: 14) and Oklahoma (Stitt 1977: 50, pl. 2: 1), they may prove to represent species of separate but closely related genera.

Conopolus granulus n. sp.

Fig. 27.6–10

Blountiella sp. undet. – Wilson 1954: 267, pl. 24: 16

Holotype. – Cranidium (Fig. 27.7a-d), MGUH 17.376 from GGU 225529.

Material. – Ten cranidia and nine questionably assigned pygidia in GGU 225528, 225529, 225535, 225539, 225540, 225544, 225546, 225552, 225561, 225563, 271403, and 271414.

Fig. 25. *Durinia granulosa* n. gen. n. sp. and *Wandelella compta* n. gen. n. sp.

1. *Durinia granulosa* n. gen. and n. sp. Small exfoliated cranidium in dorsal (a), frontal (b), and left-lateral (c) views; MGUH 17.344 from GGU 271414, X 8.8.
2–10. *Wandelella compta* n. gen. and n. sp. 2. Incomplete cranidium resting above partly exposed pygidium; MGUH 17.345 (cranidium) and 17.346 (pygidium) from GGU 225542, X 5.5. 3. Dorsal exoskeleton lacking librigenae, meraspid degree 8(?); MGUH 17.347 from GGU 225541, X 8.8. 4. Rostral plate in external view, MGUH 17.348 from GGU 225542, X 5.5. 5. Early holaspid(?) cranidium, MGUH 17.349 from GGU 225541, X 5.5. 6. Two cranidia, larger with attached anterior part of thorax; MGUH 17.350 (right) and 17.351 (left) from GGU 225541, X 5.5. 7. Large, incomplete exoskeleton; MGUH 17.352 from GGU 225541, X 5.5. 8. Holotype dorsal exoskeleton lacking librigenae; MGUH 17.353 from GGU 225542, X 5.5. 9. Pygidium of intermediate holaspid size, resting above slightly exposed, smaller pygidium; MGUH 17.354 from GGU 225541, X 5.5. 10. Large, incomplete, dorsal exoskeleton retaining slightly displaced librigenae; MGUH 17.355 from GGU 225542, X 5.5.

Diagnosis. – *Conopolus* cranidia with short palpebral lobes; glabella of low convexity and having 1 or 2 pairs of weak, oblique backwards, lateral furrows; median tubercle on occipital ring; surface finely granulose. Pygidial characters as described for genus.

Remarks. – *C. granulus* differs from *C. rasettii* n. sp. by having a much less tumid posterior glabella and much shorter palpebral lobes. Also, *C. rasettii* lacks a tubercle on the occipital ring and it has a smooth cranidial surface.

Occurrence. – Rare in most lithofacies of the lower 111 m of the Holm Dal Formation.

Conopolus rasettii n. sp.

Undetermined cranidium No. 1 – Rasetti 1963: 593, pl. 70: 26–28

Holotype. – Cranidium, U.S. National Museum of Natural History no. 140314.

Diagnosis. – *Conopolus* having tumid posterior glabella, no lateral glabellar furrows or occipital tubercle, palpebral lobes approximately half as long as glabella, and nongranulose cranidial surface.

Remarks. – Rasetti (1963) has given a detailed description and good illustrations of the single known cranidium. Differences between *C. rasettii* and *C. granulus* are given in the discussion of *C. granulus*.

Occurrence. – Boulder M-19 (Rasetti 1963: 578) of late Middle Cambrian age from a Lower Ordovician conglomerate near Metis, western Gaspé Peninsula, Quebec, Canada.

Genus *Elrathia* Walcott 1924

Type species. – *Conocoryphe (Conocephalites) kingii* Meek 1870, p. 63.

Remarks. – The generic concept of Robison (1964: 540–541) is followed here.

Elrathia marjumi Robison 1964

Fig. 20.13, 14

Elrathia marjumi – Robison 1964: 542, pl. 85: 6–13, 20

New material. – Seven cranidia in GGU 315009 and 315011.

Remarks. – Rare, small cranidia of *Elrathia* in the Holm Dal Formation are indistinguishable from those of *E. marjumi* from Utah. The cranidia illustrated here have a less tapered glabella than that previously illustrated for the species, but a less tapered glabella is to be expected in smaller holaspides.

Occurrence. – *E. marjumi* now is known from Utah and North Greenland and has an observed stratigraphic range from the upper *Ptychagnostus atavus* to upper *Lejopyge laevigata* zones. It is rare in dark lime mudstone from about 26 to 27 m above the base of the Holm Dal Formation in Freuchen Land.

Elrathia omega n. sp.

Fig. 26.1–10

Holotype. – Exoskeleton (Fig. 26.10), MGUH 17.366 from GGU 225543.

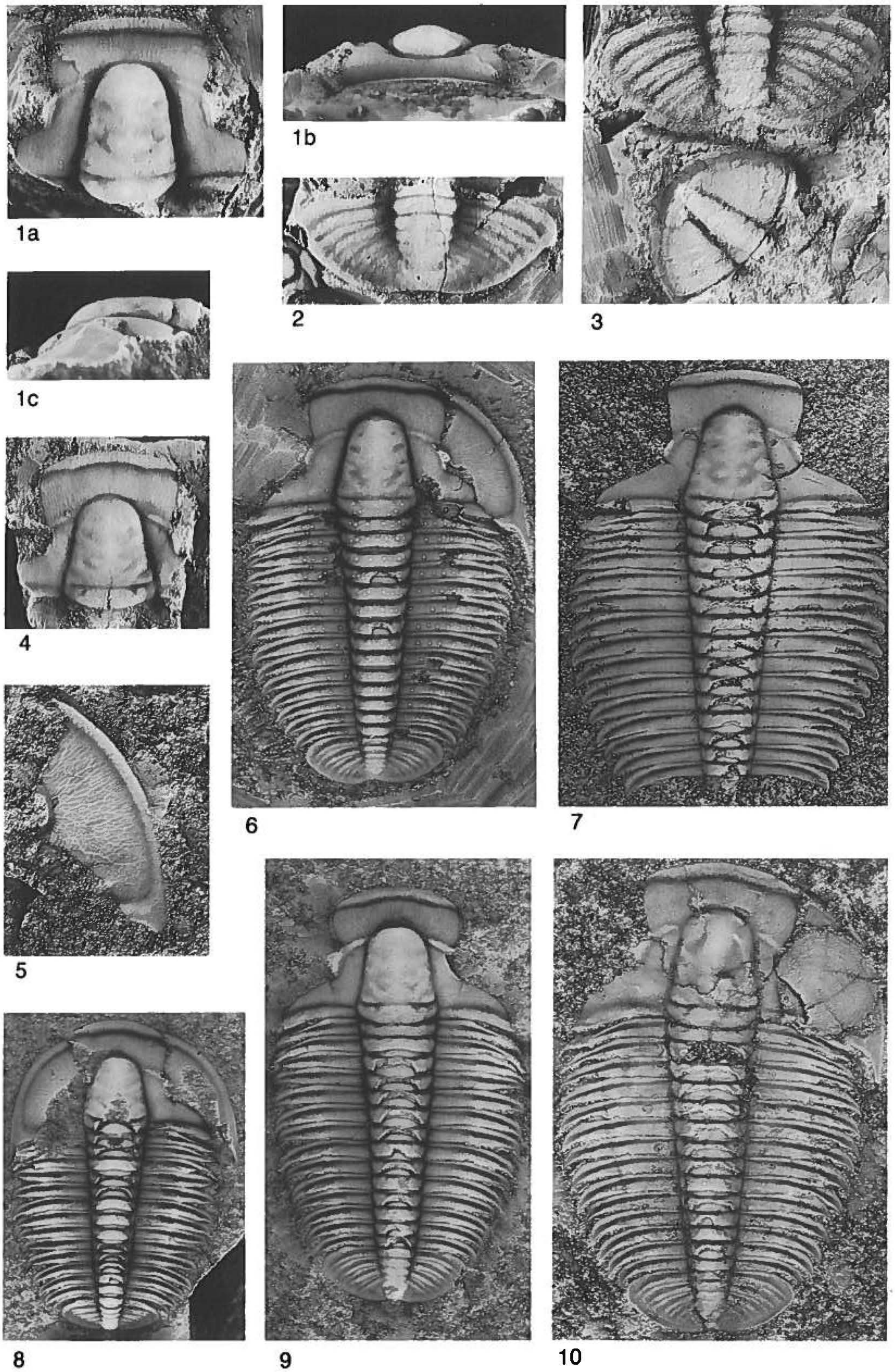
Material. – Several dorsal exoskeletons and many disarticulated sclerites in GGU 225529, 225535, 225539–225544, 225546, 225548, 225561, 225563, 225592–225595, 271403, 271414, 271417, and 315011.

Diagnosis. – Anterior border furrow of cranidium having pair of weak deflections. Axis moderately wide. Thorax with 14 segments. Pygidium alate, axis having 4 or 5 rings and short terminal piece.

Description. – *Elrathia* with axis of intermediate width. Anterior border furrow of cranidium usually having pair of slight deflections, each about halfway inward from lateral ends. Glabella commonly showing weak but complex pattern of incipient lateral furrows. Occipital

Fig. 26. *Elrathia omega* n. sp.

1–10. *Elrathia omega* n. sp. 1. Large cranidium in dorsal (a), frontal (b), and left-lateral (c) views; MGUH 17.356 from GGU 271417, X 3.3. 2. Large pygidium, MGUH 17.357 from GGU 225561, X 3.3. 3. Large pygidium (upper) associated with pygidium of *Cedaria prolifica* (lower); MGUH 17.358 (above) and 17.359 (below) from GGU 225594, X 3.3. 4. Large cranidium compressed in dark lime mudstone; MGUH 17.360 from GGU 225546, X 3.3. 5. Right librigena having anastomosing network of fine vascular ridges on surface of genal field; MGUH 17.361 from GGU 225546, X 3.3. 6. Dorsal exoskeleton lacking left librigena and having scattered granules on surface of thorax and back edge of cephalon; MGUH 17.362 from GGU 225542, X 3.3. 7. Large incomplete dorsal exoskeleton, MGUH 17.363 from GGU 225542, X 2.2. 8. Dorsal exoskeleton with damaged genae and down-flexed pygidium, MGUH 17.364 from GGU 225544, X 3.3. 9. Dorsal exoskeleton lacking librigenae, MGUH 17.365 from GGU 225543, X 3.3. 10. Holotype, dorsal exoskeleton lacking left librigena; lingulide brachiopod is superimposed on right librigena; MGUH 17.366 from GGU 225543, X 3.3.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ring having weak medial node. Eye ridge generally well developed, confluent with short palpebral lobe. Genal spine moderate in length, terminating near end of fourth thoracic segment. Thorax with 14 segments. Pygidium alate; anterolateral margins may be swollen but lack spines; posteromedian margin having broad, shallow indentation. Pygidial axis slightly tapered, containing 4 or 5 rings and short terminal piece. Pleural field commonly showing 4 pleural furrows and 3 weaker interpleural furrows. Anastomosing vascular prosopon may be weakly developed on genal field. Scattered granules rare on thorax and posterior cranidium.

Remarks. – *E. omega* and *E. marjumi* are the youngest known species of *Elrathia*. Of species presently assigned to the genus, *E. omega* is the only one known to possess 14 thoracic segments. Weak, symmetrical deflections generally characterize the anterior border furrow of the cranidium. These probably mark positions of underlying connective sutures between the rostral plate and the anterior doublure of bounding librigenae.

The pattern of incipient lateral glabellar furrows in *E. omega* is similar to that of *E. alapyge* Robison 1964, from Nevada and Utah. *E. omega*, however, has a narrower axis, one less thoracic segment, and longer genal spines.

E. omega differs from the type species, *E. kingii* by its wider axis, at least one more thoracic segment, and longer genal spines.

Some specimens of *E. omega* have rare scattered granules on the thorax and posterior cranidium. One holaspid of intermediate size (Fig. 26.6) has fairly common granules on the thorax. Although such granulation is unusual, the character is variable within the population and is not accorded taxonomic significance.

Occurrence. – *E. omega* ranges through most of the Holm Dal Formation. It is present in most lithofacies, but is most common in dark lime mudstone.

Genus *Exigua* Howell 1937

Exigua – Howell 1937: 1197; Shaw 1966a: 289
Brassicicephalus – Lochman 1940: 39; Shimer & Shrock 1944: 621; Lochman in Harrington et al. 1959: O299

Type species. – *Exigua quadrata* Howell 1937, p. 1197, pl. 6, fig. 24.

Emended diagnosis. – Small ptychoparioids known from cranidium. Glabella well defined, subquadrate to subrectangular with broadly rounded front, moderately to strongly convex, and unfurrowed. Occipital ring expanded medially. Frontal area short, convex, moderately downsloping; border furrow commonly effaced, rarely weak; sagittal width of preglabellar field about four times that of border. Pseudoborder furrow shallow at side of fixigena between border furrow and palpebral lobe. Palpebral area of fixigena horizontal to slightly downsloping, 0.5 to 0.7 times width of glabella. Palpebral lobe short, opposite anterior glabella. Anterior sections of facial suture subparallel. Border furrow of posterior fixigena widens and turns forward near abaxial end.

Remarks. – Shaw (1966a: 288–289) assigned *Exigua* and *Brassicicephalus* to the new subfamily Brassicicephalinae and concluded that "the only significant differences between the two genera are in the brim structure. In *Exigua* it is convex throughout. In *Brassicicephalus* the brim structure is concave in front of the glabella and convex anteriorly..." Shaw then expressed doubt about the generic significance of the differences, but decided against synonymy. The differences cited by Shaw appear to represent no more than minor variation in width and depth of the axial furrow in front of the glabella, in part influenced by differential exfoliation. In my opinion, these are trivial, and I here suppress *Brassicicephalus* as a subjective junior synonym of *Exigua*.

Cranidia previously assigned to either *Exigua* or *Brassicicephalus* usually have been described as having an anterior border furrow that is developed at the sides but is effaced medially. Exfoliated cranidia of *E. quebecensis* Rasetti 1946, from Greenland (e.g. Fig. 15.13) show that a narrow, weak border is evident on the internal mold, and the feature previously described as the border furrow is actually a pseudoborder furrow.

Representatives of *Exigua* are rather widespread in open-shelf lithofacies of North America and range in age from latest Middle Cambrian to early Late Cambrian. Possible cranidia of *Exigua* in Australia have been identified as *Brassicicephalus* sp. indet. by Öpik (1967: 347, pl. 36: 7, 8). Specimens from Siberia have also been assigned to *Brassicicephalus*, but were subsequently reassigned to *Letniites* by Rosova 1977: 75).

Exigua quebecensis (Rasetti) 1946

Fig. 15.12–14

Brassicicephalus quebecensis – Rasetti 1946: 448, pl. 67: 19, 20
Brassicicephalus sp. – Kindle 1982: pl. 1.2: 14

New material. – Five cranidia, one each in GGU 225528, 225535, 225548, 225552, and 271408.

Remarks. – Cranidia from Greenland agree well with Rasetti's description of the species. Exfoliated specimens, however, show separate anterior border and pseudoborder furrows. One specimen (MGUH 17.217) has weak transverse terrace lines on the lower part of the frontal area.

Occurrence. – Specimens are rare in the lower 119 m of the Holm Dal Formation, but are present in a variety of lithofacies. The species is presently known from Quebec, western Newfoundland, and North Greenland.

Genus *Hemirhodon* Raymond 1937

Type species. – *Hemirhodon schucherti* Raymond 1937, pp. 1104–1105, pl. 2, figs 12, 13.

Hemirhodon sp.

Fig. 16.1–7

Material. – Ten cranidia and 5 pygidia in GGU 225528, 225529, 225535, 225537, 225547, 225552, 225561, 225564, and 271414.

Remarks. – Rare, mostly small cranidia and pygidia of *Hemirhodon* are present in several collections. Fragments of large sclerites suggest that most of the available material represents immature individuals. Cranidia range in length from about 2 to 23 mm and are characterized by an unfurrowed, clavate glabella. Pygidia do not exceed about 4 mm in length, but show evidence of the wide doublure and several pairs of weak, subequal pleural and interpleural furrows. Assignment to a species is deferred until characters of mature holaspides become better known.

In general form, the cranidia and pygidia of *Hemirhodon* sp. conform closely to those described by Fortey (1985: 224–225) as characterizing well-streamlined, swimming trilobites. During ontogeny, the front of the cranidium is produced into an elongate snout (cf. Fig. 16.1b, 2b). Fortey mentioned that such a snout is a distinctive feature in some Ordovician genera, but he had "not been able to find any Cambrian, nor any post-Ordovician trilobite with the same modification." *Hemirhodon* sp. appears to be a good example from the late Middle Cambrian.

Occurrence. – *Hemirhodon* sp. is rare in the lower 111 m of the Holm Dal Formation, with most specimens preserved in lime grainstone.

Genus *Holmdalia* n. gen.

Type species. – *Modocia punctata* Rasetti 1967, pp. 99–100, pl. 12, figs 24–28.

Diagnosis. – Small, rather simple polymeroids. Glabella of moderate size, slightly tapering forwards, unfurrowed. Frontal area subequally divided. Pygidium having broadly rounded rear margin, one axial ring, mostly effaced axial furrow, and mostly smooth pleural region. Dorsal surfaces of cranidium and thoracic rings abundantly punctate.

Description. – Small polymeroids; maximum observed cranidial length 2.7 mm. Cranidium moderately convex. Axial furrow deep, wide. Glabella tumid, unfurrowed; subrectangular to moderately tapered forwards and broadly to sharply rounded at front. Occipital furrow deep, moderately wide, straight or slightly bowed backwards. Occipital ring simple. Frontal area subequally divided by moderately wide, deep border furrow having moderate forward curve; preglabellar field convex, downsloping; anterior border slightly upturned, tapering in width laterally. Palpebral area of fixigena slightly downsloping, width one-third to half that of adjacent glabella. Palpebral lobe short, anterior of or opposite glabellar midpoint. Eye ridge indistinct. Posterior area of fixigena transversely narrower than occipital ring; having wide, deep border furrow. Anterior sections of facial suture slightly divergent. Puncta relatively large, abundant on dorsal surface, except in furrows.

Each thoracic segment having prominent axial ring with punctate surface. Pleural furrows deep, terminating abruptly near lateral margins. Pleuron bluntly tapering forward at distal end.

Pygidium having broadly rounded posterior margin; length about one-fourth width. Axis effaced except for one ring. First ring furrow effaced laterally, well impressed medially. Axial furrow mostly effaced except for depressions at sides of single ring. Pleural region smooth except for adaxial vestige of one pleural furrow.

Remarks. – Small punctate cranidia from New York were assigned to *Modocia punctata* by Rasetti (1967), and he presumed that they were immature. Similar small cranidia are common in North Greenland. An associated incomplete, punctate thorax has an articulated pygidium with characters quite different from those typical of *Modocia*. Therefore, the new genus *Holmdalia* is established to receive these specimens, most of which seem to be holaspides.

Although cranidia of *Holmdalia* do resemble those of *Modocia*, the similarity may result more from a simplicity in general features than from close genetic relationship. The ancestry of *Holmdalia* is unclear at this time.

Holmdalia punctata (Rasetti 1967)

Fig. 27.1–5

Modocia punctata – Rasetti 1967: 99–100, pl. 12: 24–28

New material. – More than 25 cranidia in GGU 225528, 225535, 225561, and 271414. One partially enrolled, incomplete thorax with attached pygidium is in GGU 225535.

Diagnosis. – Characters of genus.

Remarks. – An incomplete thorax and attached pygidium is assigned to *H. punctata* because of size and the presence of distinctive puncta on the axial rings of the thorax. Of the many trilobite species in the Holm Dal Formation, *H. punctata* is the only one with abundant, large puncta.

During inferred holaspid ontogeny, cranidia of *H. punctata* changed in glabellar outline from subrectangular to moderately tapered with a sharply rounded front. Also, the preglabellar field had a minor increase in sagittal width relative to the anterior border, the palpebral lobes migrated slightly backwards to a position opposite the glabellar midpoint, and the palpebral area of the fixigenae had a minor increase in width relative to that of the glabella.

Occurrence. – *H. punctata* is known from the *Lejopyge laevigata* Zone of New York and North Greenland. The species is rare to common in some beds of lime grainstone and wackestone from the lower 22 m of the Holm Dal Formation.

Genus *Verditerrina* n. gen.

Type species. – *Verditerrina lacinia* n. sp.

Diagnosis. – Ptychoparioid of small size. Glabella unfurrowed, moderately tapered, truncate anteriorly. Palpebral area of fixigena steeply upsloping; palpebral lobe small, elevated, and anterior from glabellar midpoint. Frontal area moderately long, unequally divided, slightly downsloping, strongly rounded at front margin. Occipital spine moderately large.

Description. – Cranidium subtriangular in dorsal view. Axial furrow laterally broad and deep, anteriorly narrow and shallow. Glabella unfurrowed, moderately tapered, truncate anteriorly; length subequal to posterior width and about half that of cranidium exclusive of occipital spine. Occipital furrow of medium depth. Occipital ring extending posteromedially into stout, obliquely upward projecting spine. Frontal area slightly downsloping; divided by narrow, shallow, nearly straight border furrow. Preglabellar field having low transverse anterior convexity, upturned posterolaterally. Anterior border medially broad, gently convex transversely and longitudinally; length (sag.) slightly less than that of preglabellar field; anterior margin strongly rounded. Palpebral area of fixigena about equal in width to adjacent glabella, steeply upsloping. Palpebral lobe short, anterior from glabellar midpoint, and elevated above glabella. Posterior area of fixigena straplike; width (tr.) about twice that of posterior glabella, narrow (exsag.), crossed obliquely by deep border furrow that is widest in midcourse. Anterior sections of facial suture moderately convergent; posterior sections strongly divergent, sinuous. Dorsal surface smooth except for rare, scattered granules of moderate size.

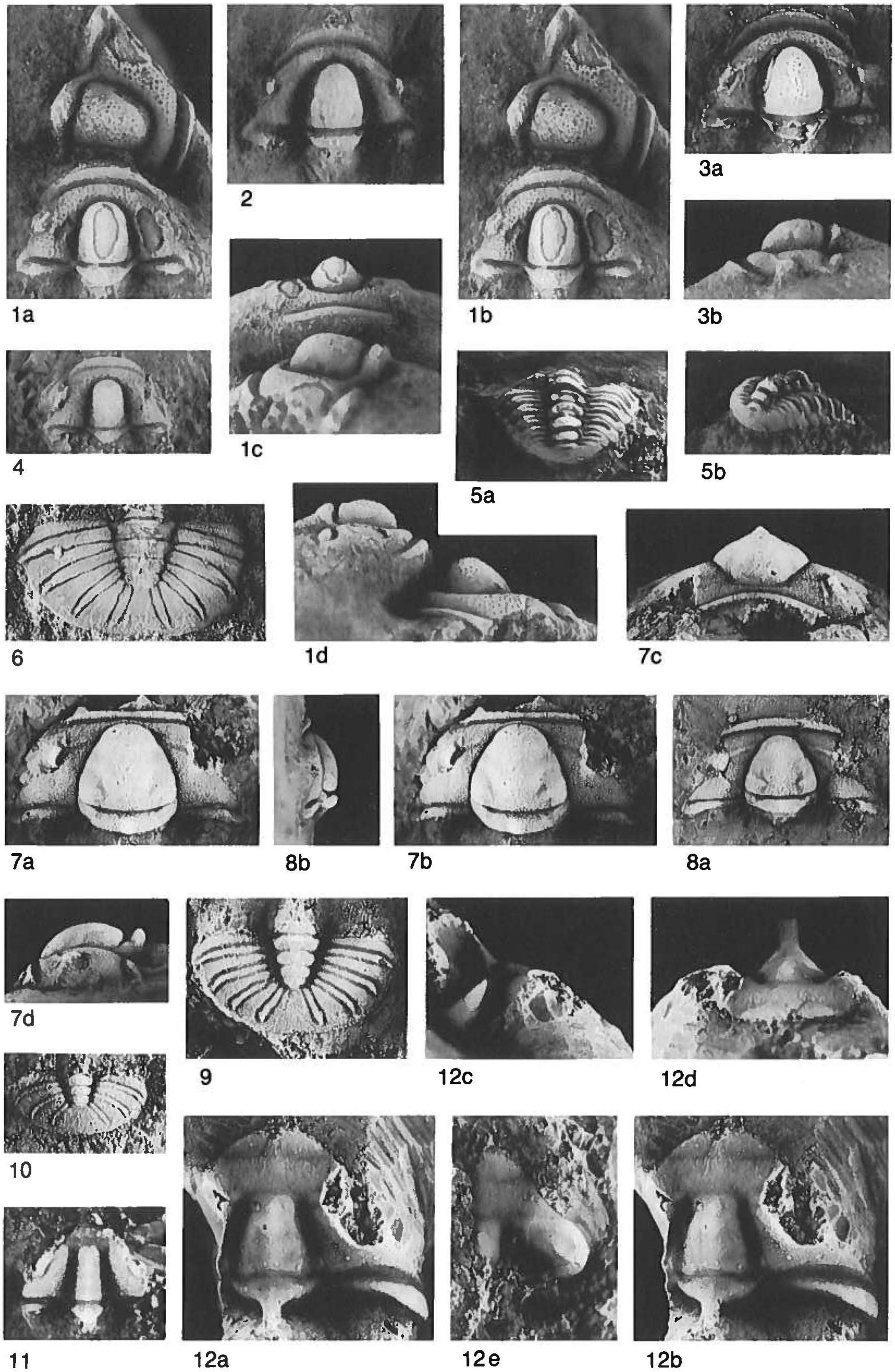
Remarks. – Two cranidia, one immature, can not readily be assigned to any trilobite genus. Because of the distinctive combination of characters listed in the diagnosis, I assign these specimens to *Verditerrina* n. gen. In glabellar form, *Verditerrina* resembles such Middle Cambrian genera as *Bolaspidella* and *Eldoradia* Resser 1935. It differs from *Bolaspidella*, however, by its longer and much more evenly sloping frontal area, more elevated palpebral lobes, and greater effacement of lateral glabellar furrows. In glabellar structure, *Verditerrina* is closely similar to *Eldoradia*, but otherwise differs by its lack of a medial boss on the preglabellar field, a nearly straight anterior border furrow, wider (sag.) an-

Fig. 27. *Holmdalia punctata* (Rasetti), *Conopolus granulus* n. gen. n. sp. and *Verditerrina lacinia* n. gen. n. sp.

1–5. *Holmdalia punctata* (Rasetti), n. gen. 1. Two mostly testaceous cranidia in stereo (a, b), frontal (c, upper), and right-lateral (d, upper) views; MGUH 17.367 (upper) and 17.368 (lower) from GGU 225535, X 13.2. 2. Large, mostly exfoliated cranidium with tapered glabella; MGUH 17.369 from GGU 225561, X 8.8. 3. Exfoliated cranidium in dorsal (a) and left-lateral (b) views, MGUH 17.370 from GGU 271414, X 13.2. 4. Small holaspid(?) cranidium with subrectangular glabella, MGUH 17.371 from GGU 225535, X 13.2. 5. Pygidium and articulated posterior part of thorax in dorsal (a) and right-oblique (b) views, MGUH 17.372 from GGU 225535, X 13.2.

6–10. *Conopolus granulus* n. gen. and n. sp. 6, 9, 10. Pygidia of decreasing size, which are questionably assigned to this species; MGUH 17.373–17.375 from GGU 271414, 225552, and 271414 respectively, all X 6.6. 7. Holotype cranidium in stereo (a, b), frontal (c), and left-lateral (d) views; MGUH 17.376 from GGU 225529, X 6.6. 8. Cranidium in dorsal (a) and left-lateral (b) views, MGUH 17.377 from GGU 225544, X 5.5.

11, 12. *Verditerrina lacinia* n. gen. and n. sp. 11. Cranidium, probably early holaspid; MGUH 17.378 from GGU 225535, X 13.2. 12. Holotype cranidium in stereo (a, b), right-lateral (c), and frontal (d) views; a latex cast of counterpart (e) shows part of right fixigena with palpebral lobe; MGUH 17.379 from GGU 225535, X 7.7.


1a
2
1b
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3b
1c
4
5a
5b
6
1d
7c
7a
8b
7b
8a
7d
9
12c
12d
10
11
12a
12e
12b

terior border, and presence of an occipital spine. Because structures of the trilobite axis, corresponding to important body organs, are likely to be more significant than those of the pleural lobes (Henningsmoen 1951, Rasetti 1954), they commonly have been given more weight in phyletic evaluation. Thus, on the basis of comparative axial structure, I suggest that *Verditerrina* may have its closest affinity with *Eldoradia*.

Verditerrina lacinia n. sp.

Fig. 27.11, 12

Holotype. – Cranidium (Fig. 27.12a-e), MGUH 17.379 from GGU 225535.

Material. – Two cranidia in GGU 225535.

Description. – Characters of genus.

Remarks. – The immature cranidium (Fig. 27.11) is probably an early holaspid. Compared to the holotype, it has a longer axis and shorter frontal area, a less developed occipital spine, and shows vestiges of at least four glabellar segments.

Occurrence. – Rare in lime grainstone from about 22 m above the base of the Holm Dal Formation.

Genus *Wandelella* n. gen.

Type species. – *Wandelella compta* n. sp.

Diagnosis. – Opisthoparian ptychopariid with 11 thoracic segments. Sagittal width of preglabellar field about four times that of narrow anterior border. Lateral glabellar furrows weak, posterior pair bigeniculate to bifurate. Pygidium nearly half as long as cephalon, semicircular, nonspinose; as many as seven segments developed on axis and pleural fields. Prosopon including vascular network on genal fields and scattered as well as regularly arranged granules on various exoskeletal surfaces.

Description. – Cephalon having narrow, well-defined axial furrow. Glabella slightly tapered forward, moderately rounded anteriorly. Lateral glabellar furrows weakly to moderately developed; S1 bigeniculate to bifurate, oblique backwards; S2 straight to slightly convex, oblique backwards, or rarely pitlike; S3 weakly evident only on largest holaspides. Occipital furrow narrowing and shallowing medially. Occipital ring with small median node in front of midpoint. Anterior sections of facial suture slightly divergent, straight or slightly convex; posterior sections moderately divergent, convex. Palpebral area of fixigena slightly convex, width about half that of occipital ring. Palpebral lobe about one-third length of glabella, posterior end opposite glabellar midpoint. Eye ridge prominent, straight or slightly curved, approximately transverse. Preglabellar field gently downsloping. Anterior border narrow, upturned; width (sag.) about one-fourth that of preglabellar field. Librigena having narrow lateral border and wide posterior border; genal spine short, extending back to third thoracic segment.

Thorax containing 11 segments. Pleural tips falcate.

Pygidium semicircular, width slightly greater than twice length. Axis slightly tapered, terminating just short of posterior pygidial margin; containing 4 to 7 rings and short terminal piece, number of rings increasing during holaspid ontogeny. Pleural field having well-developed pleural furrows and only slightly less well-developed interpleural furrows, numbers corresponding to number of axial rings; successive furrows progressively more obliquely curved; course of some interpleural furrows interrupted by minor irregularities. Narrow border may be defined by slight change in surface slope; outer margin smooth, having broad but shallow medial indentation.

Exoskeleton thin, maximum observed length almost 20 mm. Surface of genal field covered with abundant, fine, anastomosing vascular prosopon; prominence increasing during ontogeny. Cephalic surface, except furrows, having scattered granules of moderate size. Thoracic segments commonly having paired as well as scattered granules on axial ring and row of somewhat evenly spaced granules along posterior pleural edges. Surface of pygidium continuing pattern of thoracic granules except that axial rings have only one medial pair.

Remarks. – The phyletic affinities of *Wandelella* are unclear. The general cephalic aspect superficially resembles that of *Pianaspis* Saito & Sakakura 1936, but the number of thoracic segments in *Wandelella* is considerably fewer and the pygidium differs greatly in relative size and general structure. These genera probably are not closely related, and I am at a loss to suggest a family assignment for *Wandelella*.

Wandelella presently includes only the type species, *W. compta* from North Greenland.

Wandelella compta n. sp.

Fig. 25.2–10

Holotype. – Exoskeleton without librigenae (Fig. 25.8), MGUH 17.353 from GGU 225542.

Material. – Several partial exoskeletons and more than 50 disarticulated sclerites in GGU 225539–225544, 225546, 315007, and 315013.

Description. – Characters of genus.

Remarks. – Most of the specimens of *W. compta* have been compressed in fine-grained matrix. A common medial deepening of the anterior axial furrow of the cephalon (e.g. Fig. 25.10) and a rarely present, narrow, transverse, preglabellar ridge (Fig. 25.2) are probably secondary compressional features.

Occurrence. – *W. compta* is rare to common in dark lime mudstone from 48 to 111 m above the base of the Holm Dal Formation.

Undetermined pygidium

Fig. 20.15

Remarks. – A single, distinctive, alaform pygidium is present in GGU 225547. All dorsal furrows are either very weak or effaced. Its broad, convex axis tapers only slightly and extends to the posterior margin. Wide pleural regions are almost flat and slightly downsloping except for abruptly upturned margins. In general aspect, the pygidium resembles that of *Carinamala longispina* Palmer 1962, but has a wider axis and more upturned margins. It is preserved in lime grainstone from about 111 m above the base of the Holm Dal Formation.

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References

Angelin, N. P. 1851. Palaeontologia Suecica, pars I, crustaceorum formationis transitionis. – Stockholm: 24 pp.
Bambach, R. K., Scotese, C. R. & Ziegler, A. M. 1980. Before Pangea: the geographies of the Paleozoic world. – Am. Scient. 68: 26–38.
Belt, T. 1867. On some new trilobites from the Upper Cambrian rocks of north Wales. – Geol. Mag. 4: 294–295.
Beyrich, E. 1845. Ueber einige böhmische Trilobiten. Berlin [Not seen; cited by Westergård 1946]
Brøgger, W. C. 1878. Om paradoxideskifrene ved Krekling. – Nyt Mag. Naturvid. 24: 18–88.
Brongniart, A. 1822. Les Trilobites. In: Brongniart, A. & Desmarest, A.-G. Histoire naturelle des crustacés fossiles. – F. G. Levrault, Paris: 154 pp.
Bruton, D. L., Harper, D. A. T., Gunby, I. & Naterstad, J. 1984. Cambrian and Ordovician fossils from the Hardangervidda Group, Haukelifjell, southern Norway. – Norsk geol. Tidsskr. 64: 313–324.
Butts, C. 1926. The Paleozoic rocks. In: Adams, G. I. et al. Geology of Alabama. – Spec. Rep. geol. Surv. Ala. 14: 41–230.
Chang, W. T. 1980. A review of the Cambrian of China. – J. geol. Soc. Aust. 27: 137–150.
Chernysheva, N. E. (ed.) 1960. Principles of paleontology: arthropods, trilobites and crustaceans. – Gosudar. Nauchno-Tekh. Izd. Lit. Geol. Okhr. Nedr., Moscow: 515 pp. [In Russian]
Chu Chao-ling 1965. Some Middle Cambrian trilobites from Huzhu, Tsinghai. – Acta palaeont. Sin. 13: 145–155.
Daily, B. & Jago, J. B. 1975. The trilobite *Lejopyge* Hawle & Corda and the Middle-Upper Cambrian boundary. – Palaeontology 18: 527–550.
Dalman, J. W. 1828. Årsberättelse om nyare zoologiska arbeten och upptäcker. – Vet. Acad. Årsber., Stockholm: 138 pp.
Dawson, J. W. 1868. Acadian geology. The geological structure, organic remains, and mineral resources of Nova Scotia, New Brunswick, and Prince Edward Island, 2nd ed. – Macmillan, London: 694 pp.
Deiss, C. 1939. Cambrian stratigraphy and trilobites of northwestern Montana. – Spec. Pap. geol. Soc. Am. 18: 135 pp.
Derby, J. R. 1966. Paleontology and stratigraphy of the Nolichucky Formation (Cambrian) in southwest Virginia and northeast Tennessee. – Unpublished Ph.D. dissertation, Virginia Polytechnic Institute and State University: 468 pp.
Eby, R. G. 1981. Early Late Cambrian trilobite faunas of the Big Horse Limestone and correlative units in central Utah and Nevada. – Unpublished Ph.D. dissertation, State University of New York, Stony Brook: 613 pp.
Egorova, L. I., Xiang Liwen, Lee Shangi, Nan Ronshan & Kuo Zhengming 1963. Cambrian trilobite fauna from Kwenchow and western Hunan. – Chinese Acad. Geol. Sci., Ministry of Geology. China Industrial Press, Beijing. Stratigr. Palaeont. 3(1): 117 pp. [In Chinese]
Egorova, L. I., Shabanov, Y. Y., Pegel, T. V., Savitsky, V. E., Suchov, S. S. & Chernysheva, N. E. 1982. Maya Stage of type locality (Middle Cambrian of Siberian platform). – Trudy Akad. Nauk SSSR, Minist. Geol., Mezhbedom. Stratigr. Kom. SSSR 8: 146 pp. [In Russian]
Eldredge, N. 1970. Observations on burrowing behavior in *Limulus polyphemus* (Chelicerata, Merostomata), with implications on the functional anatomy of trilobites. – Am. Mus. Novit. 2436: 17 pp.
Ergaliev, G. K. 1980. Middle and Upper Cambrian trilobites of the Lesser Karatau Range. – Akad. Nauk Kazakh. SSR, Inst. Geol., Alma-Ata: 210 pp. [In Russian]
Fortey, R. A. 1985. Pelagic trilobites as an example of deducing the life habits of extinct arthropods. – Trans. R. Soc. Edinb. 76: 219–230.
Grönwall, K. A. 1902. Bornholms Paradoxideslag og deres fauna. – Danm. geol. Unders. 13: 230 pp.
Harrington, H. J. 1938. Sobre las faunas del Ordoviciano inferior del norte Argentino. – Revta Mus. La Plata, N S 1: 109–289.
Harrington, H. J. & 17 others 1959. Arthropoda 1. In: Moore, R. C. (ed.), Treatise on invertebrate paleontology, Part O. – Geol. Soc. Am. and Kansas Univ. Press, Lawrence, Kansas: 560 pp.
Hawle, I. & Corda, A. J. C. 1847. Prodrom einer Monographie der böhmischen Trilobiten. – Abh. K. böhm. Ges. Wiss. 5: 176 pp.
Henningsmoen, G. 1951. Remarks on the classification of trilobites. – Norsk geol. Tidsskr. 29: 174–217.
Henningsmoen, G. 1957. The trilobite family Olenidae. – Skr. norske Vidensk-Akad. Mat.-naturv. Kl. 1: 303 pp.
Hicks, H. 1872. On some undescribed fossils from the Menevian Group. – Q. Jl geol. Soc. Lond. 28: 173–185.
Holm, G. & Westergård, A. H. 1930. A Middle Cambrian fauna from Bennett Island. – Mem. Acad. Sci. l'URSS 21 (8): 1–25.
Hood, K. C. & Robison, R. A. this volume. Trilobite and lithofacies relationships in the Holm Dal Formation (late

Middle Cambrian), central North Greenland. – Meddr Grønland, Geosci.
Horný, R. & Bastl, F. 1970. Type specimens of fossils in the National Museum, Prague. Vol. 1, Trilobita. – National Museum, Prague: 359 pp.
Howell, B. F. 1935a. New Middle Cambrian agnostian trilobites from Vermont. – J. Paleont. 9: 218–221.
Howell, B. F. 1935b. Some New Brunswick Cambrian agnostians. – Bull. Wagner Free Inst. Sci. 10(2): 13–16.
Howell, B. F. 1937. Cambrian *Centropleura vermontensis* fauna of northwestern Vermont. – Bull. geol. Soc. Am. 48: 1147–1210.
Howell, B. F. 1955. *Phalagnostus,* new genus for trilobite *Battus nudus* Beyrich. – J. Paleont. 29: 925–926.
Hu, Chung-Hung 1964. The ontogeny and dimorphism of *Welleraspis lata* Howell (Trilobita). – J. Paleont. 38: 95–97.
Hu, Chung-Hung 1968. Notes on the ontogeny and sexual dimorphism of Upper Cambrian trilobites of the *Welleraspis* faunule from Pennsylvania. – J. Nanyang Univ. 2: 321–357.
Hu, Chung-Hung 1969. Ontogeny and sexual dimorphism of three Upper Cambrian trilobites. – J. Nanyang Univ. 3: 438–462.
Hu, Chung-Hung 1971. Ontogeny and sexual dimorphism of lower Paleozoic Trilobita. – Palaeontogr. Am. 7(44): 27–155.
Hu, Chung-Hung 1972. Ontogeny of three *Cedaria* Zone trilobites from Upper Cambrian, Montana. – Trans. Proc. Palaeont. Soc. Japan, N S 85: 245–259.
Hu, Chung-Hung 1985. Ontogenetic development of Cambrian trilobites from British Columbia and Alberta, Canada (Part I). – J. Taiwan Mus. 38(2): 121–158.
Hu, Chung-Hung 1986. Ontogenetic development of Cambrian trilobites from British Columbia and Alberta, Canada (Part II). – J. Taiwan Mus. 39(1): 1–44.
Hupé, P. 1953. Classification des trilobites. – Annales Paléont. 39: 59–168.
Hutchinson, R. D. 1962. Cambrian stratigraphy and trilobite faunas of southeastern Newfoundland. – Bull. geol. Surv. Can. 88: 156 pp.
Illing, V. C. 1916 [dated 1915]. Paradoxidian fauna of the Stockingford Shales. – Q. Jl geol. Soc. Lond. 71: 386–415.
Ineson, J. R. this volume. Lithostratigraphy and depositional setting of the Holm Dal Formation (Middle Cambrian), central North Greenland. – Meddr Grønland, Geosci. 20.
Ivshin, N. K. 1953. Middle Cambrian trilobites of Kazakhstan, part I. – Akad. Nauk Kazakh. SSR, Alma-Ata: 226 pp. [In Russian]
Jaekel, O. 1909. Über die Agnostiden. – Z. dt. geol. Ges. 61: 380–401.
Jago, J. B. 1976. Late Middle Cambrian agnostid trilobites from north-western Tasmania. – Palaeontology 19: 133–172.
Jago, J. B. 1977. A late Middle Cambrian fauna from the Que River beds, western Tasmania. – Pap. Proc. R. Soc. Tasmania 111: 41–57.
Jell, P. A. 1986. An early Late Cambrian trilobite faunule from Kashmir. – Geol. Mag. 123: 487–492.
Khairullina, T. I. 1970. Trilobites of the Maiskov Stage of the Turkestan Mountains. – In: Shayukuboe, T. S. (ed.), Biostratigraphy of the sedimentary area of Uzbekistan. – Nedra 9, Leningrad: 5–53. [In Russian]. Not seen; cited Zool. Rec. 1979, 112(11): 4
Khairullina, T. I. 1973. Biostratigraphy and trilobites of the Maiskov Stage, Middle Cambrian of the Turkestan Mountains. – FAN Uzbek. SSR, Tashkent: 112 pp. [In Russian]
Kindle, C. H. 1982. The C. H. Kindle collection: Middle Cambrian to Lower Ordovician trilobites from the Cow Head Group, western Newfoundland. – Current Research, Geol. Surv. Can., Pap. 82-1C: 1–17.
Kobayashi, T. 1935. The Cambro-Ordovician formations and faunas of South Chosen. Palaeontology. Part III. Cambrian faunas of South Chosen with a special study on the Cambrian trilobite genera and families. – J. Fac. Sci., Tokyo Univ. 4(2): 49–344.
Kobayashi, T. 1937. The Cambro-Ordovician shelly faunas of South America. – J. Fac. Sci., Tokyo Univ. 4(4): 369–522.
Kobayashi, T. 1939a. On the agnostids (Part 1). – J. Fac. Sci., Tokyo Univ. 5(5): 70–198.
Kobayashi, T. 1939b. Supplementary notes on the Agnostida. – J. geol. Soc. Japan 46: 577–580.
Kobayashi, T. 1942. An occurrence of dolichometopids in South Chosen with a summary note on the classification of the Dolichometopinae. – J. geol. Soc. Japan 49(591): 468–475.
Lake, P. 1906. A monograph of the British Cambrian trilobites, part 1. – Monogr. Palaeontogr. Soc., London: 28 pp.
Lazarenko, N. P. & Datsenko, V. A. 1967. Biostratigraphy of the Upper Cambrian of the northwestern Siberian platform. – Uch. Zap. Nauchno-Issled. Inst. Geol. Arktiki, Paleont. i Biostratig. 20: 13–32. [In Russian]
Lazarenko, N. P. & Nikiforov, N. I. 1968. Trilobite assemblage from the Upper Cambrian deposits of the Kulyurne River (northwestern Siberian platform). – Uch. Zap. Nauchno-Issled. Inst. Geol. Arktiki, Paleont. i Biostratig. 23: 20–80. [In Russian]
Lermontova, E. V. 1940. Arthropoda. – In: Vologdin, A. (ed.), Atlas of the leading forms of the fossil faunas of the USSR. Vol. 1. – Gos. Izd. Geol. Lit., Moscow-Leningrad: 112–157. [In Russian]
Lin Tian-rui, Lin Huan-ling & Zhou Tian-yong 1983. Discovery of the Cambrian trilobites in Kunshan of southeast Jiangsu with reference to the faunal provinciality and palaeogeography. – Acta palaeont. Sin. 22: 399–412. [In Chinese with English summary]
Linnarsson, J. G. O. 1869. Om Vestergötlands Cambriska och Siluriska aflagringar. – K. Svenska Vetensk.-Akad. Handl. 8(2): 1–89.
Liu Yiren 1982. Trilobita. – In: Palaeontological atlas of Hunan – Mem. Geol. Bur. Hunan 2(1): 290–347. [In Chinese]
Lochman, C. 1936. New trilobite genera from the Bonneterre Dolomite (Upper Cambrian) of Missouri. – J. Paleont. 10: 35–43.
Lochman, C. 1938. Middle and Upper Cambrian faunas from western Newfoundland. – J. Paleont. 12: 461–477.
Lochman, C. 1940. Fauna of the basal Bonneterre Dolomite (Upper Cambrian) of southeastern Missouri. – J. Paleont. 14: 1–53.
Lochman, C. 1950. Upper Cambrian faunas of the Little Rocky Mountains, Montana. – J. Paleont. 24: 322–349.
Lochman, C. & Duncan, D. 1944. Early Upper Cambrian faunas of central Montana. – Spec. Pap. geol. Soc. Am. 54: 181 pp.
Lochman, C. & Hu, Chung-Hung 1960. Upper Cambrian faunas from the northwest Wind River Mountains, Wyoming: Part I. – J. Paleont. 34: 793–834.
Lochman, C. & Hu, Chung-Hung 1961. Upper Cambrian faunas from the northwest Wind River Mountains, Wyoming: Part II. – J. Paleont. 35: 125–146.
Lochman, C. & Hu, Chung-Hung 1962. Upper Cambrian faunas from the northwest Wind River Mountains, Wyoming: Part III. – J. Paleont. 36: 1–28.
Lochman-Balk, C. & Wilson, J. L. 1958. Cambrian biostratigraphy in North America. – J. Paleont. 32: 312–350.
Lu Yen-hao 1957. Trilobita. – In: Index fossils of China, Invertebrata. 3. Geological Press, Peking: 249–294. [In Chinese]
Lu Yen-hao, Chang Wen-tang, Chu Chao-ling, Chien Yi-yuan & Hsiang Lee-wen 1965. Fossils of each group of China: Chinese trilobites. – Science Publication Company, Peking: vol. 1: 1–362; vol. 2: 363–766. [In Chinese]
Lu Yen-hao, Chu Chao-ling, Chien Yi-yuan, Lin Huan-ling, Chow Tse-yi & Yuen Ke-hsing 1974. Bio-environmental control hypothesis and its application to Cambrian biostratigraphy and palaeozoogeography. – Mem. Nanking Inst. Geol. Palaeont. 5: 27–126. [In Chinese]
Lu Yen-hao & Lin Huan-ling 1983. Zonation and correlation

of Cambrian faunas in western Zhejiang. – Acta geol. Sin. 57(4): 317–328. [In Chinese with English summary]
Martinsson, A. 1974. The Cambrian of Norden. – In: Holland, C. H. (ed.), Cambrian of the British Isles, Norden, and Spitsbergen. – John Wiley & Sons, London: 185–283.
McNamara, K. J. 1986. The role of heterochrony in the evolution of Cambrian trilobites. – Biol. Rev. 61: 121–156.
Meek, F. G. 1870. Descriptions of fossils collected by the U.S. Geological Survey under the charge of Clarence King, esq. – Proc. Acad. Nat. Sci. Philadelphia (2nd ser.) 14: 56–64.
Meek, F. G. 1873. Preliminary paleontological report, consisting of lists of fossils, with remarks on the age of the rocks in which they were found. – U.S. geol. Surv. Terr. 6th Ann. Rept.: 429–518.
Meek, F. G. 1877. Paleontology. – U.S. geol. Explor. 40th Parallel 4(1): 1–17.
Meek, F. G. & Hayden, F. V. 1861. Descriptions of new lower Silurian (Primordial), Jurassic, Cretaceous and Tertiary fossils collected in Nebraska Terr. – Proc. Acad. Nat. Sci. Philadelphia (2d Ser.) 5: 415–447.
Miller, B. M. 1936. Cambrian trilobites from northwestern Wyoming. – J. Paleont. 10: 23–34.
Müller, K. J. & Walossek, D. 1987. Morphology, ontogeny, and life habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden. – Fossils & Strata 19: 124 pp.
Nicholas, T. C. 1916 dated 1915. Notes on the trilobite fauna of the Middle Cambrian of the St. Tudwal's Peninsula (Carnarvonshire). – Q. Jl geol. Soc. Lond. 71: 451–472.
Öpik, A. A. 1961. The geology and palaeontology of the headwaters of the Burke River, Queensland. – Bur. Miner. Resour. Aust. Bull. 53: 249 pp.
Öpik, A. A. 1967. The Mindyallan fauna of north-western Queensland. – Bur. Miner. Resour. Aust. Bull. 74; v. 1: 404 pp.; v. 2: 167 pp., 67 pls.
Öpik, A. A. 1970. Nepeid trilobites of the Middle Cambrian of northern Australia. – Bur. Miner. Resour. Aust. Bull. 113: 48 pp.
Öpik, A. A. 1979. Middle Cambrian agnostids: systematics and biostratigraphy. – Bur. Miner. Resour. Aust. Bull. 172; vol. 1: 188 pp.; vol. 2: 67 pls.
Owen, D. D. 1852. Report of a geological survey of Wisconsin, Iowa, and Minnesota and incidentally of a portion of Nebraska Territory. – Philadelphia: 638 pp.
Palmer, A. R. 1954. An appraisal of the Great Basin Middle Cambrian trilobites described before 1900. – U.S. geol. Surv. Prof. Pap. 264-D: 55–86.
Palmer, A. R. 1955 dated 1954. The faunas of the Riley Formation in central Texas. – J. Paleont. 28: 709–786.
Palmer, A. R. 1960. Trilobites of the Upper Cambrian Dunderberg Shale, Eureka district, Nevada. – U.S. geol. Surv. Prof. Pap. 334-C: 53–109.
Palmer, A. R. 1962. *Glyptagnostus* and associated trilobites in the United States. – U.S. geol. Surv. Prof. Pap. 374: 49 pp.
Palmer, A. R. 1965. Trilobites of the Late Cambrian Pterocephaliid Biomere in the Great Basin, United States. – U.S. geol. Surv. Prof. Pap. 493: 105 pp.
Palmer, A. R. 1968. Cambrian trilobites of east-central Alaska. – U.S. geol. Surv. Prof. Pap. 559B: 115 pp.
Palmer, A. R. 1973. Cambrian trilobites. – In: Hallam, A. (ed.), Atlas of palaeobiogeography. – Elsevier, Amsterdam: 3–11.
Palmer, A. R. 1974. Search for the Cambrian world. – Am. Scient. 62: 216–224.
Palmer, A. R. 1979. Cambrian. – In: Robison, R. A. & Teichert, C. (eds), Treatise on invertebrate paleontology, part A, biogeography and biostratigraphy. – Geol. Soc. Am. & Kansas Univ., Lawrence, Kansas: A119-A135.
Palmer, A. R. & Peel, J. S. 1981. Dresbachian trilobites and stratigraphy of the Cass Fjord Formation, western North Greenland. – Bull. Grønlands geol. Unders. 141: 46 pp.
Peel, J. S. this volume. Molluscs of the Holm Dal Formation (late Middle Cambrian), central North Greenland. – Meddr Grønland, Geosci. 20.
Pokrovskaya, N. V. 1958. Middle Cambrian agnostids of Yakutia, Part I. – Trudy Geol. Inst., Akad. Nauk SSSR 16: 96 pp.
Poulsen, C. 1960. Fossils from the late Middle Cambrian *Bolaspidella* Zone of Mendoza, Argentina. – Mat.-Fys. Medd. Danske Vid. Selsk. 32: 42 pp.
Poulsen, V. 1969. An Atlantic Middle Cambrian fauna from North Greenland. – Lethaia 2: 1–14.
Qian Yi-yuan & Zhou Ze-min 1984. Middle and early Upper Cambrian trilobites from Kunshan, Jiangsu, with reference to their distribution in the lower Yangtze region. – Acta palaeont. Sin. 23: 170–184. [In Chinese with English abstract]
Qiu Hong-an & 10 others 1983. Trilobita. – In: Paleontological atlas of East China, Vol. I, Early Paleozoic – Nanjing Inst. Miner. Resour. Geological Publishing House, Beijing: 28–254. [In Chinese]
Ramos, V. A., Jordan, T. E., Allmendinger, R. W., Mpodozis, C., Kay, S. M., Cortes, J. M. & Palma, A. 1986. Paleozoic terranes of the central Argentine-Chilean Andes. – Tectonics 5: 855–880.
Rasetti, F. 1946. Early Upper Cambrian trilobites from western Gaspé. – J. Paleont. 20: 442–462.
Rasetti, F. 1948. Middle Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea). – J. Paleont. 22: 315–339.
Rasetti, F. 1954. Phylogeny of the Cambrian trilobite family Catillicephalidae and the ontogeny of *Welleraspis*. – J. Paleont. 28: 599–612.
Rasetti, F. 1956. Revision of the trilobite genus *Maryvillia* Walcott. – J. Paleont. 30: 1266–1269.
Rasetti, F. 1963. Middle Cambrian ptychoparioid trilobites from the conglomerates of Quebec. – J. Paleont. 37: 575–594.
Rasetti, F. 1965. Upper Cambrian trilobite faunas of northeastern Tennessee. – Smithson. misc. Collns 148(3): 127 pp.
Rasetti, F. 1967. Lower and Middle Cambrian trilobite faunas from the Taconic sequence of New York. – Smithson. misc. Collns 152(4): 111 pp.
Raymond, P. E. 1937. Upper Cambrian and Lower Ordovician Trilobita and Ostracoda from Vermont. – Bull. geol. Soc. Am. 48: 1079–1146.
Raymond, P. E. 1938. Nomenclature note. – Bull. geol. Soc. Am. 48 suppl.: xv (only).
Repina, L. N., Petrunina, Z. E. & Khairullina, T. I. 1975. Trilobites. – In: Repina, L. N. et al. Stratigraphy and fauna of the Lower Paleozoic of the northern submontane belt of Turkestan and the Alai ridges (southern Tian-Shan). – Trudy Inst. Geol. Geofiz., Akad. Nauk SSSR, Sibir. Otdel. 278: 100–233. [In Russian]
Resser, C. E. 1935. Nomenclature of some Cambrian trilobites. – Smithson. misc. Collns 93(5): 46 pp.
Resser, C. E. 1937. Third contribution to nomenclature of Cambrian trilobites. – Smithson. misc. Collns 95(22): 29 pp.
Resser, C. E. 1938. Cambrian System (restricted) of the southern Appalachians. – Spec. Pap. geol. Soc. Am. 15: 140 pp.
Resser, C. E. 1942. New Upper Cambrian trilobites. – Smithson. misc. Collns 103(5): 136 pp.
Resser, C. E. & Howell, B. F. 1938. Lower Cambrian *Olenellus* Zone of the Appalachians. – Bull. geol. Soc. Am. 49: 195–248.
Ritterbush, L. A. 1983. Position of the labrum in agnostid trilobites. – Lethaia 16: 309–310.
Robison, R. A. 1960. Some Dresbachian and Franconian trilobites of western Utah. – Research Stud. Brigham Young Univ. Geology Ser. 7(3): 59 pp.
Robison, R. A. 1964. Late Middle Cambrian faunas from western Utah. – J. Paleont. 38: 510–566.
Robison, R. A. 1971. Additional Middle Cambrian trilobites from the Wheeler Shale of Utah. – J. Paleont. 45: 796–804.

Robison, R. A. 1972a. Hypostoma of agnostid trilobites. – Lethaia 5: 239–248.
Robison, R. A. 1972b. Mode of life of agnostid trilobites. – Proc. 24 Internatl geol. Congr. (Montreal) 7: 33–40.
Robison, R. A. 1976. Middle Cambrian trilobite biostratigraphy of the Great Basin. – Geology Stud. Brigham Young Univ. 23(2): 93–109.
Robison, R. A. 1984. Cambrian Agnostida of North America and Greenland, Part I, Ptychagnostidae. – Paleontol. Contr. Univ. Kansas Pap. 109: 59 pp.
Romanenko, E. V. 1977. Cambrian trilobites from sections on the Bolshaya Ishe River (northeastern Altai). – In: Chernysheva, N. E. & Rosova, A. V. (eds), Biostratigraphy and fauna of the Upper Cambrian and its boundary layers. – Trudy Inst. Geol. Geofiz., Akad. Nauk SSSR, Sibir. Otdel. 313: 161-183. [In Russian]
Rosova, A. V. 1964. Biostratigraphy and description of trilobites of the Middle and Upper Cambrian of the northwestern Siberian platform. – Inst. Geol. Geofiz., Akad. Nauk SSSR, Sibir. Otdel.: 148 pp. [In Russian]
Rosova, A. V. 1977. Upper Cambrian and Lower Ordovician of the Rubnoi, Khartaiki, Kureiki and Letnei river basins. – In: Chernysheva, N. E. & Rosova, A. V. (eds), Biostratigraphy and fauna of the Upper Cambrian and its boundary layers. – Trudy Inst. Geol. Geofiz., Akad. Nauk SSSR, Sibir. Otdel. 313: 54–84. [In Russian]
Rusconi, C. 1952. Varias especies de trilobitas del Cámbrico de Canota. – Revta Mus. Hist. nat. Mendoza 6: 5–18.
Rusconi, C. 1954. Trilobitas Cámbricos de la Quebradita Oblicua, sud del Cerro Aspero. – Revta Mus. Hist. nat. Mendoza 7: 3–59.
Rusconi, C. 1955. Fósiles Cámbricos y Ordovicios al oeste de San Isidro, Mendoza. – Revta Mus. Hist. nat. Mendoza 8: 3–64.
Rushton, A. W. A. 1978. Fossils from the Middle-Upper Cambrian transition in the Nuneaton district. – Palaeontology 21: 245–283.
Rushton, A. W. A. 1979. A review of the Middle Cambrian Agnostida from the Abbey Shales, England. – Alcheringa 3: 43–61.
Rushton, A. W. A. 1983. Trilobites from the Upper Cambrian *Olenus* Zone in central England. – Spec. Pap. Palaeontology 30: 107–139.
Saito, K. & Sakakura, K. 1936. Description de deux nouvelles espèces de Trilobite: 112–117. – In: Sakakura, K., Le Cambrien du côté sud-oriental de la Pli-faille inverse de Zidô, Heian-ando, Corée. – J. geol. Soc. Japan 43(509): 104–117.
Savazzi, E. 1985. Functional morphology of the cuticular terraces in burrowing terrestrial brachyuran decapods. – Lethaia 18: 147–154.
Schmalfuss, H. 1978. Constructional morphology of cuticular terraces in trilobites, with conclusions on synecological evolution. – Neues Jb. Geol. Paläeont. Abh. 157: 164–168.
Schmalfuss, H. 1981. Structure, patterns and function of cuticular terraces in trilobites. – Lethaia 14: 331–341.
Shah, S. K. & Sudan, C. S. 1982. *Bolaspidella* from the Cambrian of Kashmir and its stratigraphic significance. – J. geol. Soc. India 23: 236–245.
Shaw, A. B. 1952. Paleontology of northwestern Vermont. II. Fauna of the Upper Cambrian Rockledge Conglomerate near St. Albans. – J. Paleont. 26: 458–483.
Shaw, A. B. 1956. Notes on *Modocia* and Middle Cambrian trilobites from Wyoming. – J. Paleont. 30: 141-145.
Shaw, A. B. 1966a. Paleontology of northwestern Vermont. X. Fossils from the (Cambrian) Skeels Corners Formation. – J. Paleont. 40: 269–295.
Shaw, A. B. 1966b. Paleontology of northwestern Vermont. XI. Fossils from the Middle Cambrian St. Albans Shale. – J. Paleont. 40: 843–858.
Shergold, J. H. 1977. Classification of the trilobite *Pseudagnostus*. – Palaeontology 20: 69–100.
Shimer, H. W. & Shrock, R. R. 1944. Index fossils of North America. – Wiley & Sons, New York: 837 pp.
Stitt, J. H. 1977. Late Cambrian and earliest Ordovician trilobites, Wichita Mountains area, Oklahoma. – Bull. Okla geol. Surv. 124: 79 pp.
Strand, T. 1929. The Cambrian beds of the Mjøsen district in Norway. – Norsk geol. Tidsskr. 10: 308–365.
Sun, Y. C. 1924. Contributions to the Cambrian faunas of north China. – Palaeont. sin. B, 1(4): 1–110.
Tasch, P. 1951. Fauna and paleoecology of the Upper Cambrian Warrior Formation of central Pennsylvania. – J. Paleont. 25: 275–306.
Taylor, K. & Rushton, A. W. A. 1972 [dated 1971]. The pre-Westphalian geology of the Warwickshire coalfield. – Bull. geol. Surv. Gt Br. 35: 150 pp.
Tullberg, S. A. 1880. Om *Agnostus*-arterna i de Kambriska aflagringarne vid Andrarum. – Sver. geol. Unders. Avh. C, 42: 37 pp.
Vogdes, A. W. 1892. On the North American species of the genus *Agnostus*. – Am. Geol. 9: 377–396.
Wahlenberg, G. 1818. Petrificata telluris Svecanae. – Nova Acta R. Soc. Sci. Upsala. 8: 116 pp.
Walcott, C. D. 1884. The paleontology of the Eureka district, Nevada. – Monogr. U.S. geol. Surv. 8: 298 pp.
Walcott, C. D. 1886. Second contribution to the studies on the Cambrian faunas of North America. – Bull. U.S. geol. Surv. 30: 369 pp.
Walcott, C. D. 1899. Cambrian fossils [of the Yellowstone National Park]. – Monogr. U.S. geol. Surv. 32: 440–479.
Walcott, C. D. 1911. Cambrian geology and paleontology II, No. 4, Cambrian faunas of China. – Smithson. misc. Collns 57(4): 69–108.
Walcott, C. D. 1916a. Cambrian geology and paleontology III, No. 3, Cambrian trilobites. – Smithson. misc. Collns 64(3): 157–258.
Walcott, C. D. 1916b. Cambrian geology and paleontology III, No. 5, Cambrian trilobites. – Smithson. misc. Collns 64(5): 301–488.
Walcott, C. D. 1924. Cambrian geology and paleontology V, No. 2, Cambrian and lower Ozarkian trilobites. – Smithson. misc. Collns 75(2): 53–60.
Walcott, C. D. 1925. Cambrian geology and paleontology V, No. 3, Cambrian and Ozarkian trilobites. – Smithson. misc. Collns 75(3): 61–146.
Wallerius, I. D. 1895. Undersökningar öfver zonen med *Agnostus laevigatus* i Vestergötland, jämte en inledande öfversikt af Vestergötlands samtliga Paradoxideslager. Gleerupska Universitets-Bokhandeln, Lund: 72 pp.
Wallerius, I. D. 1930. Från Västergötlands mellankambrium. – Geol. For. Stockh. Forh. 52: 47–62.
Wang Yu (ed.) 1964. A handbook of fossils in southeastern China. – Science Press, Academia Sinica, Peking: 171 pp. [In Chinese]
Wang Yu (ed.) 1965. A handbook of fossils in the Yangtze faunal province. – Science Press, Academia Sinica, Peking: 188 pp. [In Chinese]
Weller, S. 1900. Descriptions of Cambrian trilobites from New Jersey, with notes on the age of the Magnesian Limestone Series. – Ann. Rep. geol. Surv. N. J., 1899: 47–53.
Westergård, A. H. 1946. Agnostidea of the Middle Cambrian of Sweden. – Sver. geol. Unders. C 477: 141 pp.
Westergård, A. H. 1947. Supplementary notes on the Upper Cambrian trilobites of Sweden. – Sver. geol. Unders. C 489: 35 pp.
Whitehouse, F. W. 1936. The Cambrian faunas of north-eastern Australia, Parts 1 and 2. – Mem. Qd Mus. 11: 59–112.
Whitehouse, F. W. 1939. The Cambrian faunas of north-eastern Australia, Part 3. – Mem. Qd Mus. N S 1: 179–282.
Whittington, H. B. 1986. Late Middle Cambrian trilobites from Zanskar, Ladakh, northern India. – Riv. It. Paleont. Strat. 92: 171–188.
Wilson, J. L. 1951. Franconian trilobites of the central Appalachians. – J. Paleont. 25: 617–654.
Wilson, J. L. 1954. Late Cambrian and Early Ordovician trilobites from the Marathon uplift. – J. Paleont. 28: 249–285.

Xiang Liwen 1981. Trilobites. – In: The Cambrian System of China. – Chinese Acad. Geol. Sci., Stratigr. China 4: 170–175, pls. 7-11. [In Chinese]
Xiang Liwen & Zhang Tai-rong 1985. Systematic descriptions of trilobites. – In: Stratigraphy and trilobite faunas of the Cambrian in the western part of the northern Tian Shan, Xinjiang. – Minist. Geol. Miner. Resour., Geol. Mem. 2(4): 64–243. [In Chinese with English summary]
Yang Jia-lu 1978. Middle and Upper Cambrian trilobites of western Hunan and eastern Guizhou. – Chinese Acad. Geol. Sci., Prof. Pap. Stratigr. Palaeont. 4: 82 pp. [In Chinese]
Yang Jia-lu 1982. Notes on the Middle Cambrian trilobite faunas from Duibian of Jiangshan, Zhejiang. – Geol. Rev. 28(4): 299–307. [In Chinese with English abstract]
Yin Gongzheng 1978. Trilobita. – In: Paleontological atlas of southwestern China, Guizhou Province. Part I, Cambrian – Devonian. – Geological Press, Peking: 385–594. [In Chinese]
Zell, M. G. & Rowell, A. J. this volume. Brachiopods of the Holm Dal Formation (late Middle Cambrian), central North Greenland. – Meddr Grønland. Geosci. 20.
Zhou Tien-mei, Liu Yi-jeng, Mong Sien-sung & Sun Zheng-hua 1977. Trilobita. – In: Wang Xiao-feng & Jin Yu-qin (eds), Palaeontological handbook of central and southern China. Part I, Early Paleozoic Era. – Sciences Press, Beijing: 104–266. [In Chinese]