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Edited by John S. Peel

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Stratigraphy and Palaeontology of the Holm Dal Formation (late Middle Cambrian), central North Greenland

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MEDDELELSER OM GRØNLAND, GEOSCIENCE 20 · 1988

The Holm Dal Formation of central North Greenland is formally proposed and its depositional history elucidated. A rich fauna of trilobites, brachiopods and molluscs, and a single association of trace fossils are described. The relationship between trilobite distribution and lithofacies is analysed.

The trilobite fauna is dominated by polymeroids that are most characteristic of the lower and middle *Cedaria* Zone (early Dresbachian) as widely applied in North America. Agnostoid species are characteristic of the upper *Lejopyge laevigata* Interval-zone, indicating a late Middle Cambrian age by correlation with the Swedish standard for north-western Europe. Twenty four of the 58 species of trilobites are new, as are 9 of the 34 genera.

Fourteen species of inarticulate brachiopods are referred to 11 genera; three species are new. One new genus and 5 new species are described among 13 species of molluscs; a new ichnospecies of the arthropod trackway *Multipodichnus* is described.

Frontispiece

View looking north along Gustav Holm Dal, across Perssuaq Gletscher (centre), J. P. Koch Fjord (left) and northern Peary Land, toward the Arctic Ocean. Cambrian – Silurian shelf sediments in the foreground and along the far side of Perssuaq Gletscher are succeeded to the north by deep-water trough sediments of similar age (islands in J. P. Koch Fjord and beyond) forming the fold belt of North Greenland. Upper Middle Cambrian strata assigned to the Holm Dal Formation outcrop on both sides of Gustav Holm Dal south of Perssuaq Gletscher (Photo: Geodetic Institute, Copenhagen).

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Contents

Introduction

It is 50 years since the Danish cartographer and geologist Lauge Koch and the crew of the Dornier-Wal seaplane 'Perssuak' alighted from alongside the base ship S.S. Gustav Holm at Kings Bay (Svalbard, Fig. 1) on a flight of discovery to North Greenland. They passed Kronprins Christian Land, flying westward across the northern part of central Peary Land as far as J. P. Koch Fjord, before turning south and east to return along the southern margin of Peary Land, leaving Greenland by the coast of Kronprins Christian Land. When they landed at Kings Bay after a journey of 2200 km taking almost 12 hours they had solved the riddle of the supposed channel which explorer Robert Peary had earlier suggested separated the north-east tip of Greenland (Peary Land) from the rest of the island. The extreme western end of this supposed seaway was found to consist of the inner part of a major fjord, earlier named in honour of another Greenland explorer, J. P. Koch (Figs 1–3). The fjord thus extended many tens of kilometres farther south than could be discerned by Lauge Koch and Knud Rasmussen in 1917, from their observation point near its mouth, or by Koch in 1921 from his viewpoint on the Inland Ice far to the south.

At the outermost point of Perssuak's flight Koch discerned and mapped the topographic depression formed by Perssuaq Gletscher, Gustav Holm Dal and the valleys to the south. The feature is clearly visible in one of the expedition's photographs (Koch 1940, fig. 51) of the inner part of J. P. Koch Fjord.

Since 1938 the area has received only rare visitors. During the Danish Peary Land Expedition 1947–50, J. C. Troelsen sledged westward along the southern margin of Peary Land to the head of J. P. Koch Fjord in the spring of 1949, making important (but unpublished) observations about the geology, including recognition of the Cambrian sequence. K. Ellitsgaard-Rasmussen passed down J. P. Koch Fjord in the spring of 1950 en route to the outer coast of Greenland. Geologists employed by the commercial Greenarctic Consortium visited the area briefly in the early 1970's, landing their reconnaissance aircraft on sand flats in Fimbuldal near the southern end of Gustav Holm Dal (Fig. 2). Peter Dawes and Anker Weidick (GGU) made a brief visit to the head of J. P. Koch Fjord in the summer of 1975, the former collecting the first Middle Cambrian fossils known from the Peary Land region (J. S. Peel in Dawes 1976). Sledge teams from 'Sirius' pass unobtrusively through the area in the course of patrolling the northern shore of Greenland.

Ten years ago the Geological Survey of Greenland initiated the first stage of a regional geological investigation of North Greenland (Washington Land - Kronprins Christian Land), the North Greenland Project 1978–1980 and 1984–1985. In addition to the preparation of maps (scale 1: 500 000), the project has produced a wealth of new information concerning the geological structure and evolution of this remote part of Greenland. Preliminary results have been published as expedition reports (Rapport Grønlands Geologiske Undersøgelse, volumes 88, 99, 106, 126, 133); an embracive study of the evolution of the Lower Palaeozoic Franklinian Basin sequence is given by Higgins et al. (in press).

By coincidence, the first camp of more than 70 field camps which I established as a participant in this project was sited in the valley to which the name Gustav Holm Dal was subsequently given (Frontispiece; Figs 1–3). Among the first fossils were trilobites and brachiopods from a dark, shaly unit eventually known as formation T2 (Ineson & Peel 1980, 1987; see also Peel 1979, 1982) and defined in the present volume as the Holm Dal Formation (Ineson, this volume).

The fossils from these earliest collections were dated as early Dresbachian, earliest Late Cambrian in terms of North American custom (A. R. Palmer in Peel 1979), and represented the second occurrence of strata of this age in Greenland (Palmer & Peel 1981). Their identification promoted recollection of the sequence during 1979, at which time J. R. Ineson (this volume) made detailed stratigraphic studies. The fossil material was examined by R. A. Robison in Copenhagen during May 1981 who recognised that the trilobite fauna combined early Dresbachian elements with agnostoid trilobites indicative of the latest Middle Cambrian Zone of *Lejopyge laevigata* of the Swedish standard sequence. It was this observation and the enthusiasm of Dick Robison to describe the trilobite fauna which ultimately led to the establishment of the present co-operative venture. At a relatively late stage, western outcrops of the formation were briefly examined during 1984 and a few collections of fossils were obtained from south-eastern Freuchen Land (Fig. 1).

Acknowledgments

Many people deserve thanks for their role in making this study possible. Apart from the contributing authors and referees, State Geologist Niels Henriksen is thanked for his organisation of the North Greenland Project, providing a logistic framework which enabled the gathering of small sample bags filled with fossils from distant corners of a remote region. Close and continuing co-operation with Jon Ineson with respect to Cambrian stratigraphy is gratefully acknowledged, as is the companionship in the field and the laboratory of geologists from Denmark and abroad.

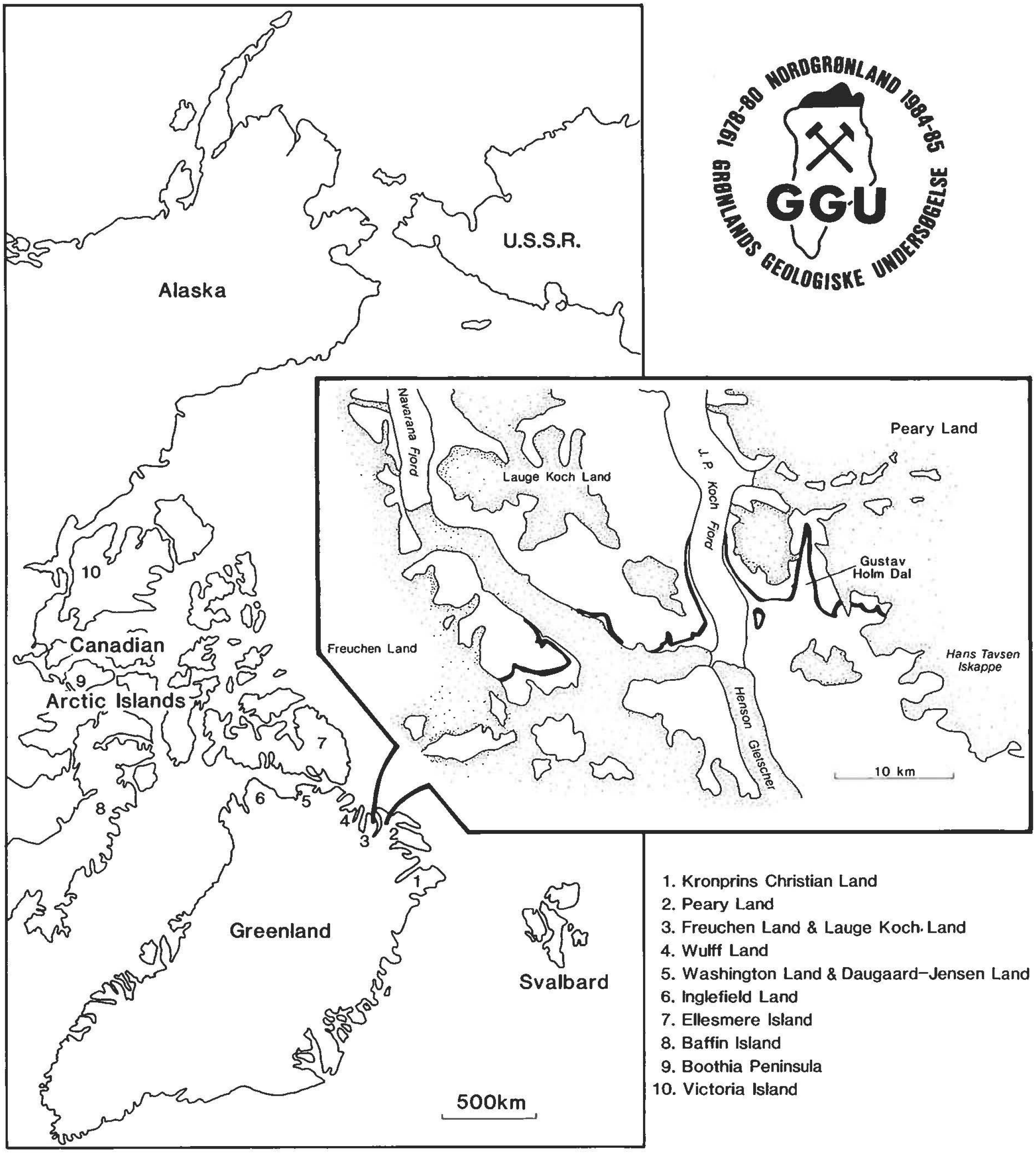

Fig. 1. Greenland viewed in polar projection showing the location of Gustav Holm Dal in the inner part of J. P. Koch Fjord. Outcrops of the Holm Dal Formation are shown in black. The formation was described and mapped during the North Greenland Project of the Geological Survey of Greenland (Grønlands Geologiske Undersøgelse, GGU), field activities of which extended from Kronprins Christian Land in the east to Washington Land in the west. The project logo is reproduced at the upper right.

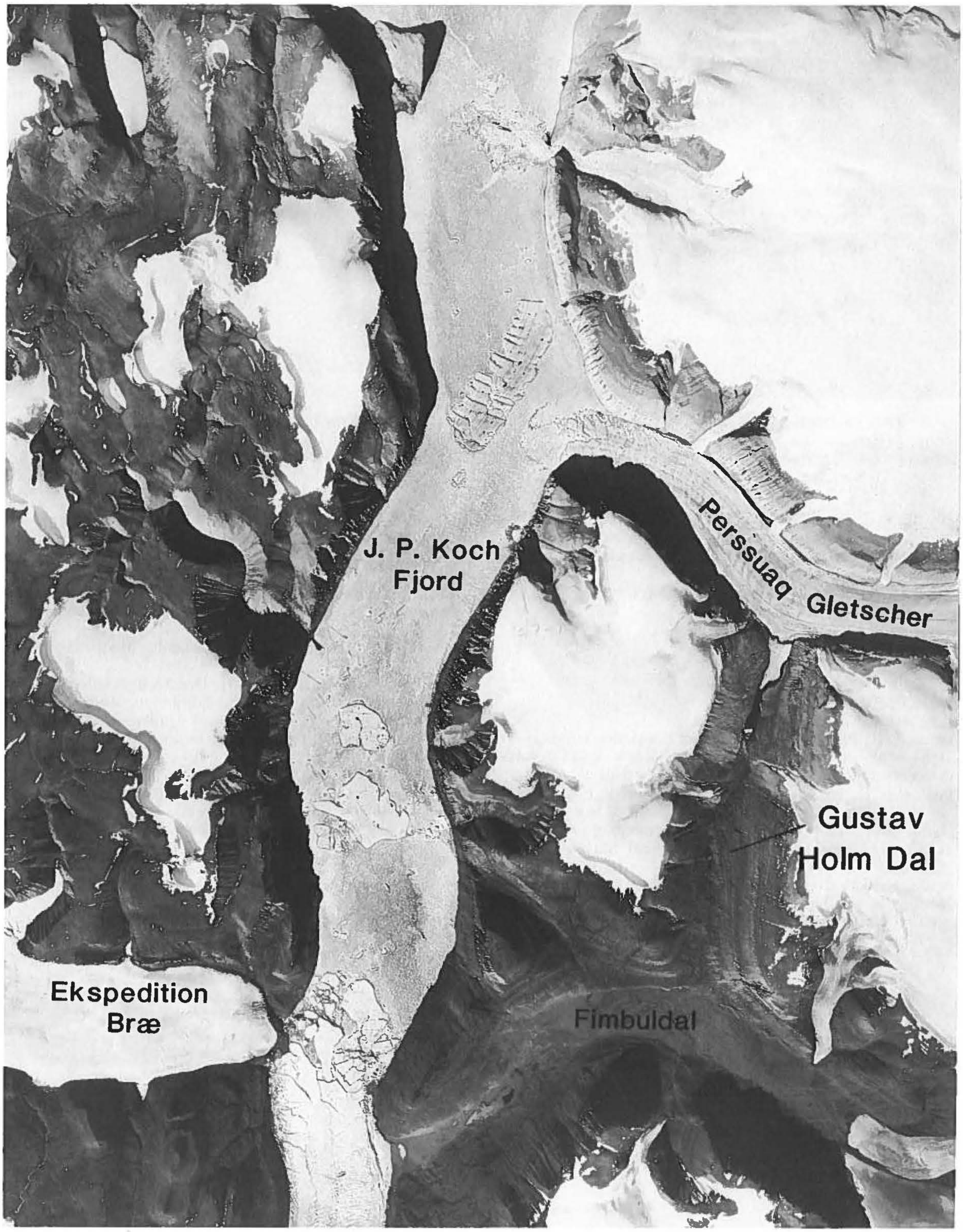

Fig. 2. Aerial photograph of the inner reaches of J. P. Koch Fjord showing Gustav Holm Dal extending north from Fimbuldal toward Perssuaq Gletscher (Copyright: Geodetic Institute, Copenhagen. Scale: 1:150 000).

Fig. 3. View eastward across J. P. Koch Fjord showing Gustav Holm Dal between the two ice caps in the middle distance. Perssuaq Gletscher lies to the left. The cliffs along J. P. Koch Fjord are in excess of 1 km high and exhibit a mainly carbonate sequence extending from the Lower Cambrian to the Middle Ordovician (Photo: Geodetic Institute, Copenhagen).

In the final compilation, Bente Thomas draughted figures which were reproduced by Jakob Lautrup and Suzanne Maling Hansen. Esben Glendal and Bodil Skall-Jensen assisted with the computer manipulation of texts.

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John S. Peel June 1988

Lithostratigraphy and depositional setting of the Holm Dal Formation (Middle Cambrian), central North Greenland

J. R. INESON

Ineson, J. R. Lithostratigraphy and depositional setting of the Holm Dal Formation (Middle Cambrian), central North Greenland. Meddr Grønland, Geosci. 20: 9–21. Copenhagen 1988-12-31.

The Holm Dal Formation (late Middle Cambrian) is formally described and assigned to the Tavsens Iskappe Group of central North Greenland. The formation consists largely of fossiliferous argillaceous lime mudstones and dolomites, interbedded at intervals with peloidal packstones and grainstones, carbonate breccia beds and sandstones. Deposition occurred mainly from suspension, but periodically also from mud-rich density currents or storm currents and viscous mass flows in a low-energy, marine outer shelf environment. The Holm Dal Formation records progressive shallowing; it represents the initial stage of a major regressive cycle that culminated in exposure of the shelf.

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The Holm Dal Formation (Middle Cambrian) is one of seven formations making up the Tavsens Iskappe Group in central North Greenland (Figs 1, 2). The carbonates and subordinate siliciclastics assigned to this group have an age range of mid Middle Cambrian to earliest Ordovician and a maximum thickness of 750 m. They form part of the Lower Palaeozoic shelf sequence of the Franklinian basin, which extends across Arctic Canada into North Greenland. These strata are bordered to the south by Precambrian sediments and gneissic basement along the fringes of the Inland Ice and to the north by deformed Lower Palaeozoic trough deposits (Figs 1, 3).

The aims of this paper are firstly to define formally the lithostratigraphy of the Holm Dal Formation and secondly to place the formation in its environmental context within the shelf sequence.

Regional setting

The Franklinian basin extends from Arctic Canada eastward across North Greenland to Kronprins Christian Land (Fig. 1). The preserved sediment column has a thickness of about 8 km and is essentially of Early Palaeozoic age, although possibly extending down into the Precambrian and up into the earliest Devonian (see Peel 1985, for review). Two distinct depositional regimes are recognised within this sequence – a southern shelf bordering the Precambrian craton and a northern deep-water trough. The shelf deposits are largely undeformed whereas the trough sediments were folded during the Devonian Ellesmerian orogeny; the degree of deformation and metamorphism increases northwards to the northern coastline of North Greenland.

The parallel evolution of shelf and trough during the Early Palaeozoic has been described by Surlyk & Hurst (1984), Hurst & Surlyk (1983) and in a recent review article by Higgins et al. (in press). Factors influencing sedimentation in the region included rifting and differential subsidence of the deep-water trough, and Caledonian uplift and nappe emplacement at the eastern limit of the basin. In particular, Surlyk & Hurst (1984) suggested that the position of the shelf-slope break at various stages in its development was governed by several east-west tectonic lineaments. The trough was restricted to northernmost North Greenland in earliest Cambrian times and expanded southwards in steps during the Early Palaeozoic as successive lineaments became active.

From the late Early Cambrian to the early Ordovician, the North Greenland shelf was composed of two major depositional settings: a shallow-water carbonate platform flanked to the north by a deeper-water outer shelf. Outer shelf deposits are a mixed siliciclastic-carbonate assemblage that grades northwards at the shelf-slope break into cherts and shales of the Cambro-Ordovician starved trough sequence (Surlyk & Hurst 1984; Higgins & Soper 1985). This simple palaeogeographic picture is complicated by lateral (east-west) variation in the subsidence history of the shelf. In the west, shelf subsidence was relatively uniform and a thick, conformable sequence of restricted platform carbonates accumulated over a wide area (Ryder Gletscher Group, see

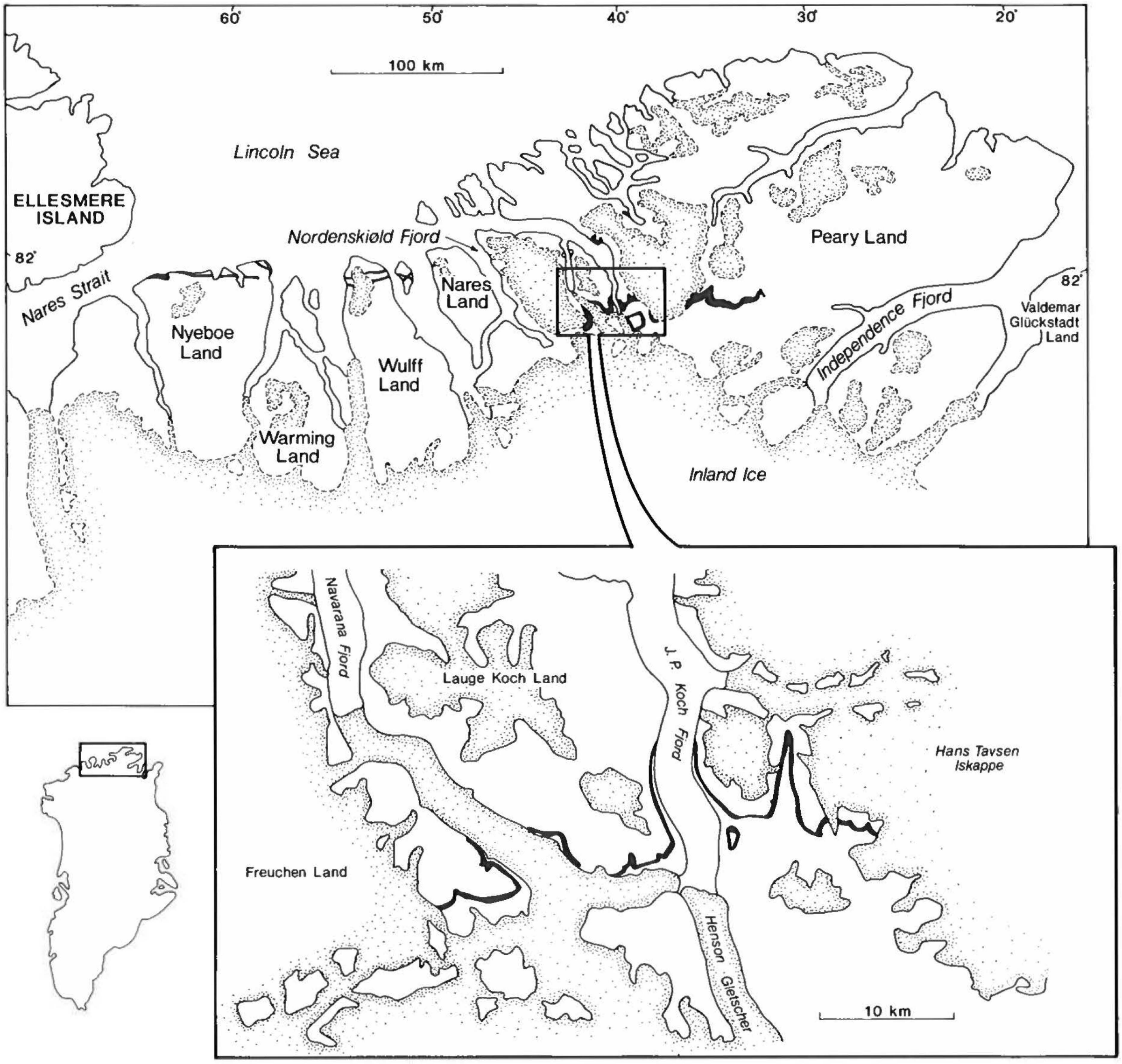

Fig. 1. Map showing the distribution of the Tavsens Iskappe Group (black) in North Greenland. Inset shows the area of outcrop of the Holm Dal Formation across west Peary Land, Lauge Koch Land and east Freuchen Land.

Figs 2, 3); coeval outer shelf deposits crop out on the north coast of Nyeboe Land and Wulff Land, near the transition into the deep-water trough (Fig. 3). Farther east, however, in Freuchen Land, Lauge Koch Land and Peary Land (Figs 1, 3), Cambrian strata record a more complex, tectonically unstable history. Uplift of the easternmost portion of the shelf, probably in response to early Caledonian events (Surlyk & Hurst 1984), resulted in tilting and progressive exposure of the shelf. Shelf subsidence was greatest in Freuchen Land and west Peary Land, where outer shelf conditions persisted over much of the region until the late Middle Cambrian (Fig. 3). Shallow-water carbonates and siliciclastics prograded intermittently northwards from the late Early Cambrian to the early Ordovician but, unlike the western platform sequence, shallow-water, platform-interior facies are only locally preserved due to progressive exposure of the platform (Fig. 3). The stratigraphic importance of the hiatus developed at the top of this regressive sequence decreases westwards and the unconformity is not recognised farther west than Nares Land (Peel & Wright 1985).

This regressive trend from outer shelf to shallow-water carbonate platform is recorded in the Brønlund Fjord and Tavsens Iskappe Groups (Fig. 4). A well-developed reciprocal sedimentation pattern is evident

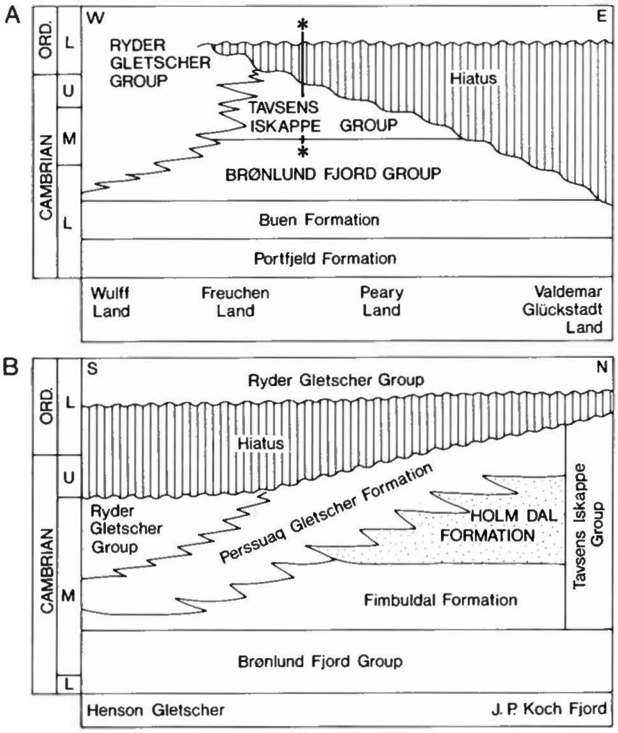

Fig. 2. A: Cambro-Ordovician lithostratigraphic relationships from Valdemar Glückstadt Land in eastern North Greenland to Wulff Land in central North Greenland. Asterisks mark the position of N-S section shown in Fig. 2B. B: Lithostratigraphic relationships of the Tavsens Iskappe Group in a N-S profile in west Peary Land, showing the stratigraphic position of the Holm Dal Formation.

within this sequence; periods of carbonate platform accretion and progradation, probably during relative sea-level highs (cf. James & Mountjoy 1983), alternated with regressive periods characterised by mixed siliciclastic-carbonate sedimentation (Fig. 4). The subject of this paper, the Holm Dal Formation, forms part of the uppermost regressive cycle and is overlain by the Perssuaq Gletscher Formation, a sequence of offlapping siliciclastics that were deposited prior to exposure of the shelf (Surlyk & Ineson 1987).

Lithostratigraphy

The Tavsens Iskappe Group was defined by Peel (1979) following fieldwork in 1978, and was discussed further by Palmer & Peel (1979); subsequently Ineson & Peel (1980) and Peel (1982) described seven informal formations within the Tavsens Iskappe Group. The formal lithostratigraphy of the Brønlund Fjord and Tavsens Iskappe Groups is presented by Ineson & Peel (in press; see Fig. 2) but the formal definition of the Holm Dal Formation is more aptly placed here to accompany the following palaeontological and biostratigraphical contributions.

Holm Dal Formation, new formation

History. – The formation has been described informally as formation 2 and formation T2 of the Tavsens Iskappe Group (Peel 1979; Ineson & Peel 1980).

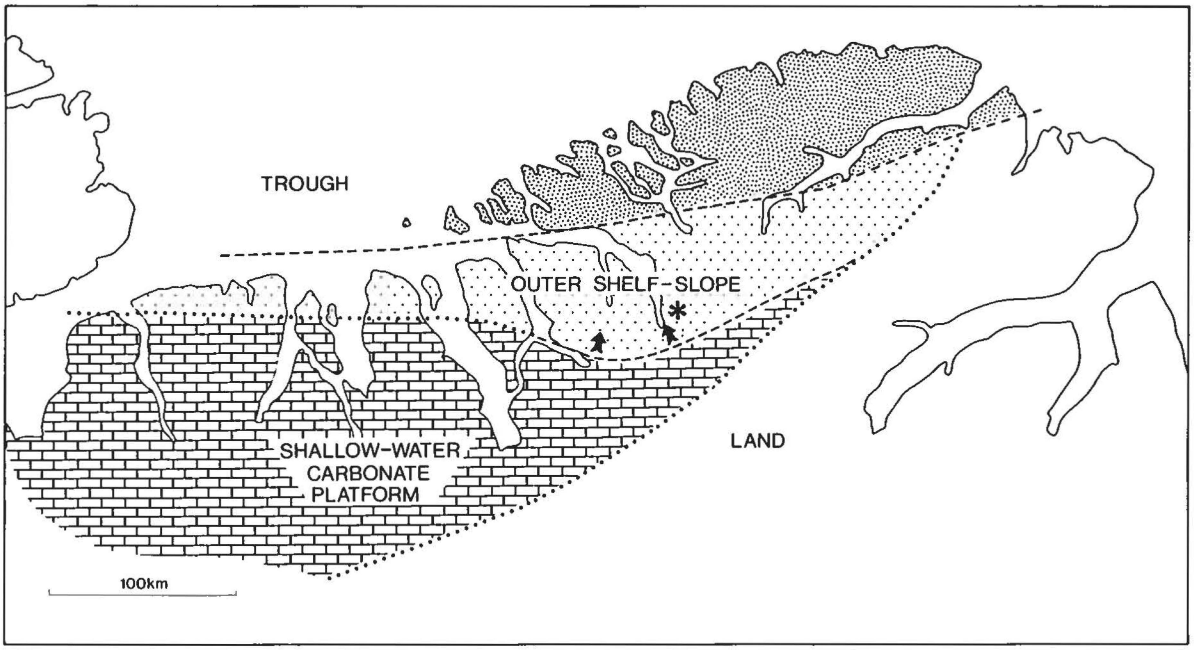

Fig. 3. Palaeogeography of North Greenland during the Middle Cambrian. Arrows show the direction of progradation of the carbonate platform; asterisk indicates the position of Gustav Holm Dal.

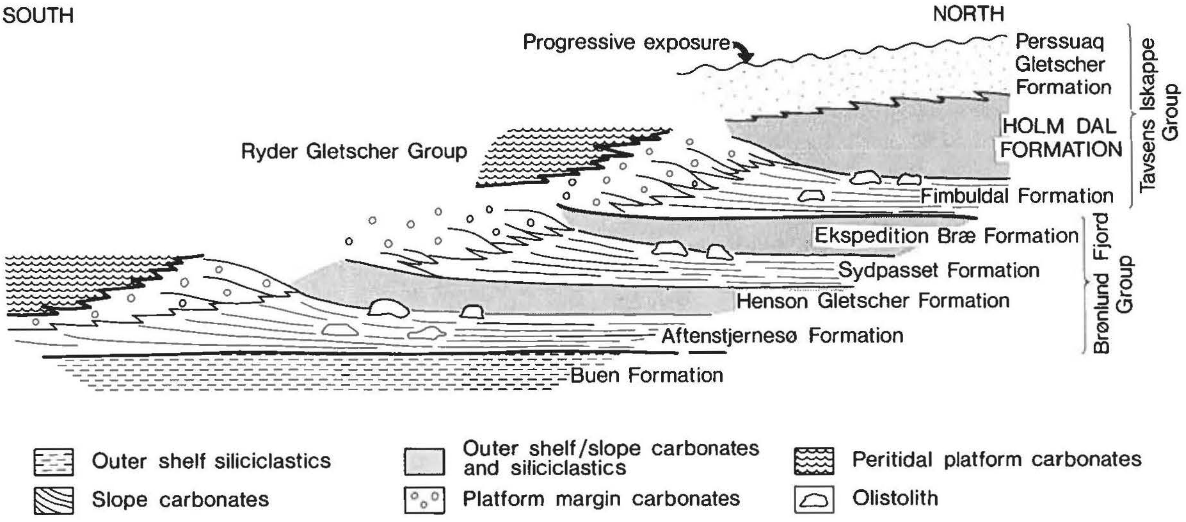

Fig. 4. Schematic diagram showing the evolution of the Cambrian shelf. Note the three major pulses in carbonate platform development, separated by mixed siliciclastic-carbonate shelf deposits.

Name. – After Gustav Holm Dal, the north-south valley linking Fimbuldal with Perssuaq Gletscher, south-west Peary Land (Figs 5, 6).

Type section. – North of the prominent gully on the east side of Gustav Holm Dal, at the junction with Fimbuldal (Figs 5–7).

Thickness. – 155 m at the type locality, thinning south and pinching out 5 km south of the type locality (Fig. 5). The formation appears to thicken northwards from the type section, but exposure is poor.

Lithology. – The Holm Dal Formation lies conformably between the Fimbuldal Formation and the Perssuaq Gletscher Formation (Figs 6, 7) and typically forms recessive dark-weathering slopes between these two pale, cliff-forming formations. The Holm Dal Formation consists largely of thin, parallel and wavy-bedded argillaceous lime mudstones and dark grey, laminated dolomites (Fig. 8). In places these fine-grained limestones are interlaminated with skeletal, peloidal packstones and grainstones. Wavy, thin-bedded peloidal grainstones, packstones and wackestones dominate the upper third of the formation, typically becoming dolomitic upwards. Silty, calcareous mudstones occur as partings and interbeds throughout the formation and quartz sandstones and siltstones are present in the upper levels (Fig. 7). Carbonate breccia beds and slumped horizons occur sporadically throughout. A detailed account of the lithofacies of the formation is given below.

Boundaries. – The base of the formation is a conformable contact, although typically abrupt (Fig. 6). The upper Fimbuldal Formation consists of massive mass-flow carbonate breccias and in many sections the top surface of these deposits is notably irregular. At the type section, this hummocky surface has a relief of up to 5 m and the basal dark, laminated dolomites of the Holm Dal Formation drape the surface topography.

The upper boundary is more complex. In vertical section it is readily placed at the conformable junction between dark, thin-bedded sandy carbonates and pale, cliff-forming carbonate breccias or sandstones (Fig. 9; see also Surlyk & Ineson 1987). On the scale of a fjord cliff-line, however, the diachroneity of this boundary is clear; pale carbonates and siliciclastics of the Perssuaq Gletscher Formation interdigitate northwards with dark carbonates of the Holm Dal Formation (Figs 4, 10). For mapping purposes, this zone of interdigitation is included in the Perssuaq Gletscher Formation.

Distribution. – The Holm Dal Formation crops out around the head of J. P. Koch Fjord in south-west Peary Land and along the cliffs flanking the glacier south of Navarana Fjord (Fig. 1). It wedges out against platform margin carbonates (Perssuaq Gletscher Formation) to the south and west and is not recognised east of Hans Tavsen Iskappe (Fig. 1). Cambrian strata dip northwards beneath Ordovician and Silurian carbonates but reappear in east-west trending anticlines near the northern coast of central North Greenland (Fig. 1; Higgins & Soper 1985). Equivalent outer shelf-slope strata in these inliers are assigned to a new formation of the Tavsens Iskappe Group (Kap Stanton Formation of Ineson & Peel, in press. Unit 3 of Higgins & Soper 1985).

Geological Age. – In its type section the Holm Dal Formation is late Middle Cambrian in age (Robison 1984, this volume). The formation contains a rich fauna

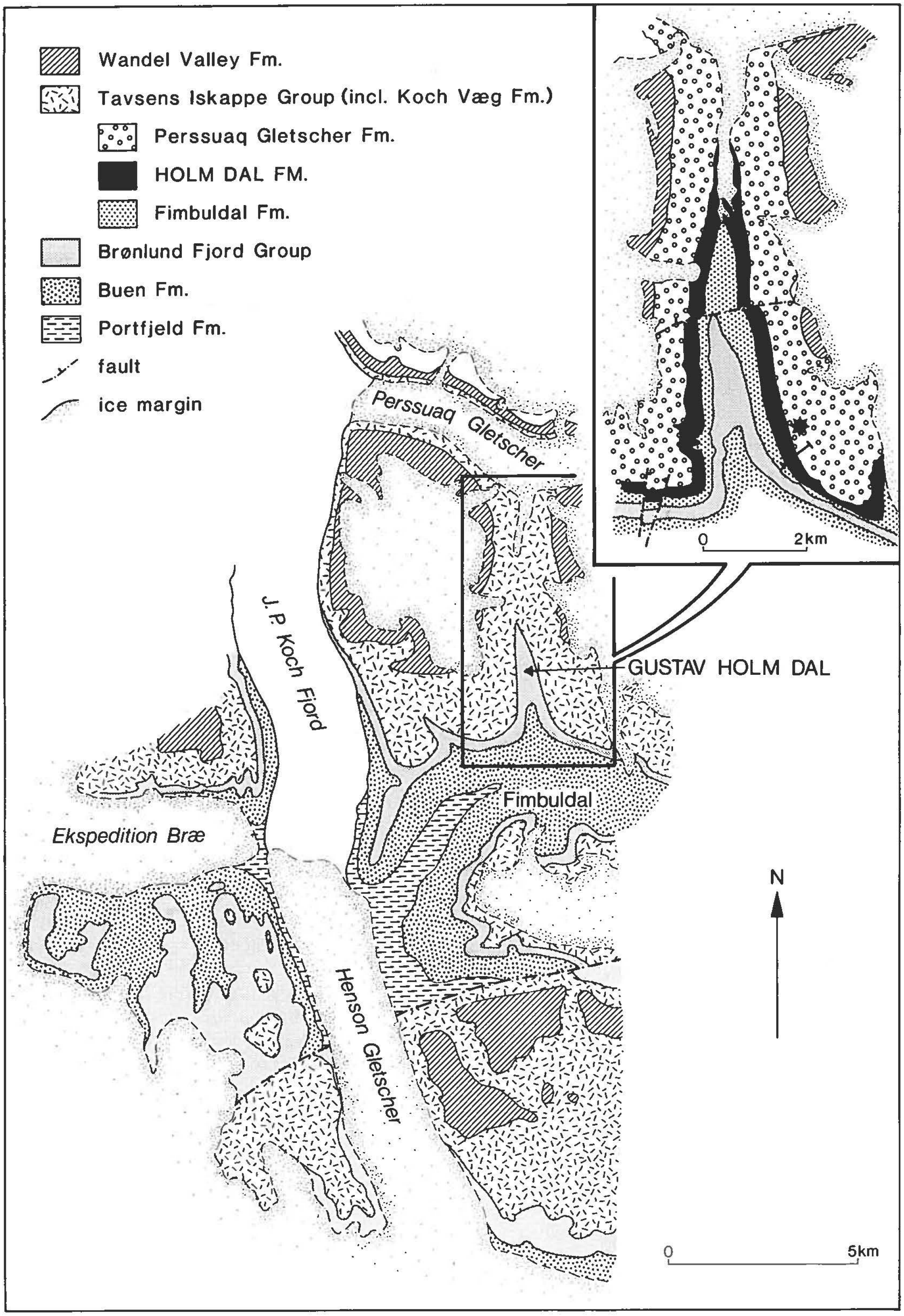

Fig. 5. Geological sketch map of the J. P. Koch Fjord region, west Peary Land. Inset of Gustav Holm Dal shows the position of the type section of the Holm Dal Formation (asterisk). The outcrop of the Tavsens Iskappe Group east of Henson Gletscher and south of the fault includes strata referred to the Koch Væg Formation of the Ryder Gletscher Group.

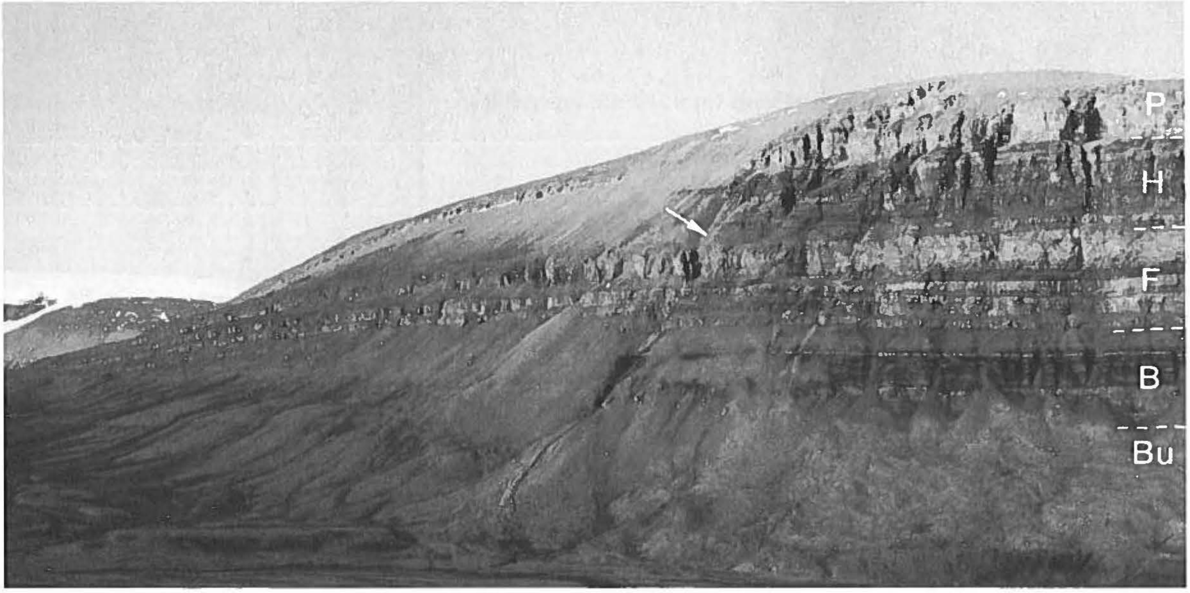

Fig. 6. The Brønlund Fjord Group (B) and Tavsens Iskappe Group (F: Fimbuldal Formation; H: Holm Dal Formation; P: Perssuaq Gletscher Formation) on the north side of Fimbuldal, west Peary Land. Bu: Buen Formation. The type section of the Holm Dal Formation is at the western (left) end of the steep cliff (arrow).

of trilobites, brachiopods and molluscs, details of which are given in accompanying papers by Robison, Hood & Robison, Zell & Rowell and Peel (this volume).

Sedimentology

The following facies analysis of the type section of the Holm Dal Formation is based primarily on the undolomitised portions of the section. Secondary dolomitisation affects nearly one third of the formation but sufficient primary fabrics and structures are retained to refer the dolomitised intervals to the following facies scheme.

Lithofacies 1, laminated silty limestones

Dark grey or black, bituminous lime mudstones show a well-developed, millimetre-scale parallel-lamination, defined by subtle variations in grain size or composition. Some laminae are picked out by quartz silt or very fine-grained sand while others show a concentration of dark bituminous matter. Brown phosphorite pellets are present in places and calcite-replaced sponge spicules are common. Siliciclastic detritus can form up to 30 % of the rock and discrete mudstone partings occur locally. Bioturbation is rare.

Interpretation. – The fine-grained, delicately laminated nature of these deposits and the absence of current-formed structures indicate deposition primarily out of suspension in a low-energy environment below wave-base. The bituminous character of these deposits, the scarcity of bioturbation and consequent preservation of fine lamination reflect oxygen-deficient bottom waters (Waples 1983; the dysaerobic-anaerobic zone of Byers 1977).

Lithofacies 2, thin-bedded argillaceous lime mudstone

This lithofacies dominates the sequence (84 % of type section, Fig. 7), forming thick, uniform intervals of alternating lime mudstone and silty, calcareous mudstone. Bedding is typically parallel (Figs 8, 11) but can be wavy or nodular; limestone beds are generally 2–5 cm thick with intervening shale partings or beds up to 5 cm thick. Limestone and shale components are well-segregated. Pressure solution features are common at bed boundaries but gradational and sharp, microscoured depositional contacts have been observed.

Limestone beds consist of weakly laminated lime mudstone, locally interlaminated with peloidal, skeletal packstone or grainstone laminae up to 1 cm thick. The lime mudstones contain up to 5 % quartz silt which in places defines a faint parallel lamination together with silt-sized micritic peloids and sponge spicules. Packstone and grainstone laminae are often broadly lenticular and in places form starved ripples. Basal contacts are sharp and sometimes scoured; coarser laminae grade up from skeletal grainstone through packstone into the overlying lime mudstone (Fig. 12). Peloids and

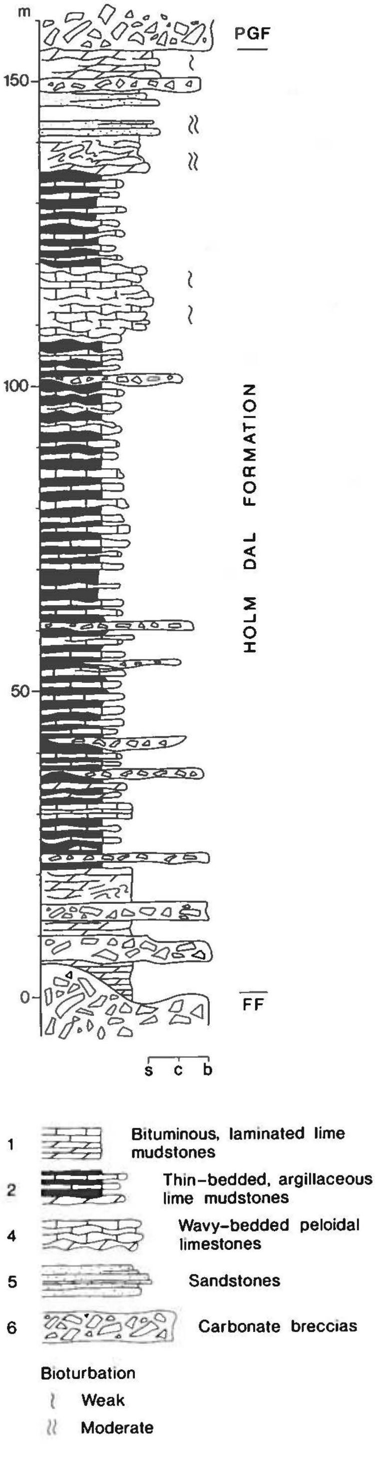

Fig. 7. Type section of the Holm Dal Formation. Numbers 1–6 refer to facies described in this paper. The limestones of the Holm Dal Formation have been locally dolomitised, indicated by oblique brick ornament. FF: Fimbuldal Formation; PGF: Perssuaq Gletscher Formation.

skeletal grains make up these grainstone laminae; the skeletal fraction is composed mainly of trilobite and phosphatic brachiopod elements together with fragments of *Girvanella* and sponge spicules. Some peloids and intraclasts are partially phosphatised. Quartz silt forms up to 30 % of the grainstone laminae.

Evidence of bioturbation is scarce in this lithofacies, the lamination is rarely disturbed and skeletal grains lie parallel with bedding.

Interpretation. – A low-energy, open marine environment is indicated by the fine-grained, fossiliferous nature of this facies and the rare evidence of current action. The scarcity of bioturbation and the presence of phosphoritic peloids and intraclasts reflect largely oxygen-deficient conditions. Lime mud was deposited mainly from suspension, probably derived from shallow-water environments during storms (cf. Neumann & Land 1975). The segregation of shale and lime mudstone is clearly diagenetic in part but probably reflects a primary fluctuation in sediment supply (cf. Brady & Koepnick 1979). The thin, silty shelly laminae record periodic action of weak tractional bottom currents that were capable of winnowing and transporting silt and sand-sized detritus. The nature of these currents is not clear; they may represent dilute density currents or the action of waves during major storms. Reworking and transport of bioclasts is also indicated by the disarticulated fragmented nature of the skeletal elements (Robison, this volume).

Comparable facies are common in 'deeper-water' carbonate sequences and are typically attributed to a deep shelf or basinal environment (e.g. Read 1980; Handford 1986).

Lithofacies 3, phosphoritic limestone

Phosphoritised intraclasts and pellets occur locally in the previous two lithofacies but a phosphorite-impregnated surface was located on frost-heaved slabs that originated within the basal 5–10 m of the formation. The finely laminated phosphoritised layer is a few millimetres thick and drapes an irregular, scoured surface. The underlying impregnated limestone is composed mainly of bioturbated skeletal wackestone or packstone with localised winnowed skeletal grainstone lags.

Interpretation. – The phosphatised surface was interpreted as a hardground, possibly formed by early diagenetic phosphorite replacement of cyanobacterial mats by Palmer et al. (1986). Exposure of the impregnated layer on the sea floor is suggested by numerous crater-like holdfasts.

The formation of phosphorite requires a slow sedimentation rate, a supply of phosphate and a reducing microenvironment (Baturin 1982). Winnowed shell lags at this horizon attest to the first of these, while reducing conditions may have been enhanced locally by the deg-

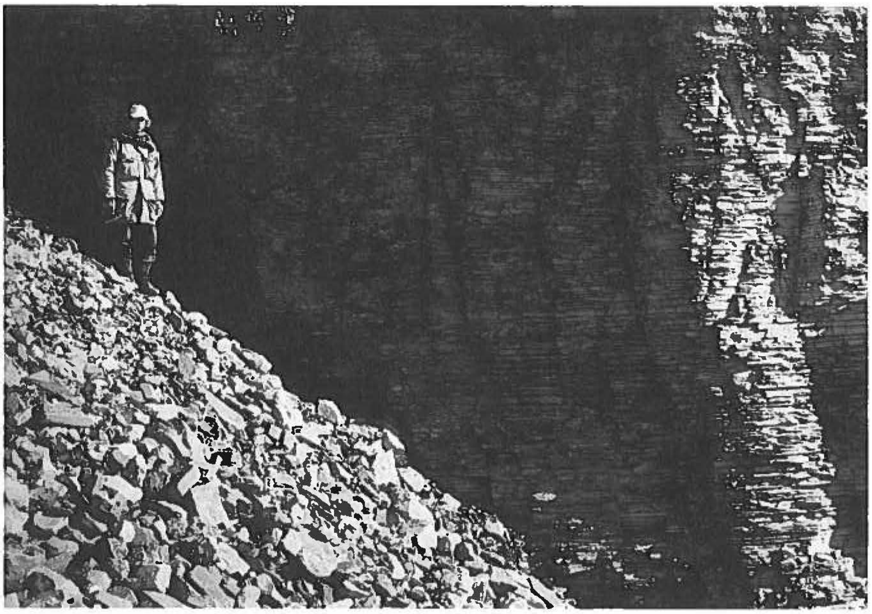

Fig. 8. Thin-bedded argillaceous lime mudstones (Lithofacies 2) near the middle of the Holm Dal Formation type section.

radation of the cyanobacterial mats. Finely laminated, bituminous carbonate forms much of the section at this stratigraphic level, reflecting the general lack of oxygen within the environment (see Lithofacies 1).

Although the exact location of this discontinous hardground could not be determined it may be significant that the basal beds of the Holm Dal Formation in this area drape the hummocky upper surface of the Fimbuldal Formation which has a relief of up to 5 m in places. Hardground development may have been favoured on these relict depositional 'highs', while mud accumulated in surrounding depressions.

Lithofacies 4, wavy-bedded peloidal limestones

Thin, wavy or nodular-bedded grey limestones in the upper third of the formation consist of fine-grained (silt-fine sand grade) packstones and grainstones, thinly interbedded with skeletal wackestones. The grainstones and packstones are composed of peloids, intraclasts and micritised skeletal grains, with an admixture of quartz silt (<5 %).

Sedimentary structures are rare, being restricted to wispy, undulating lamination; faint mottling and occasional discrete burrows attest to pervasive bioturbation.

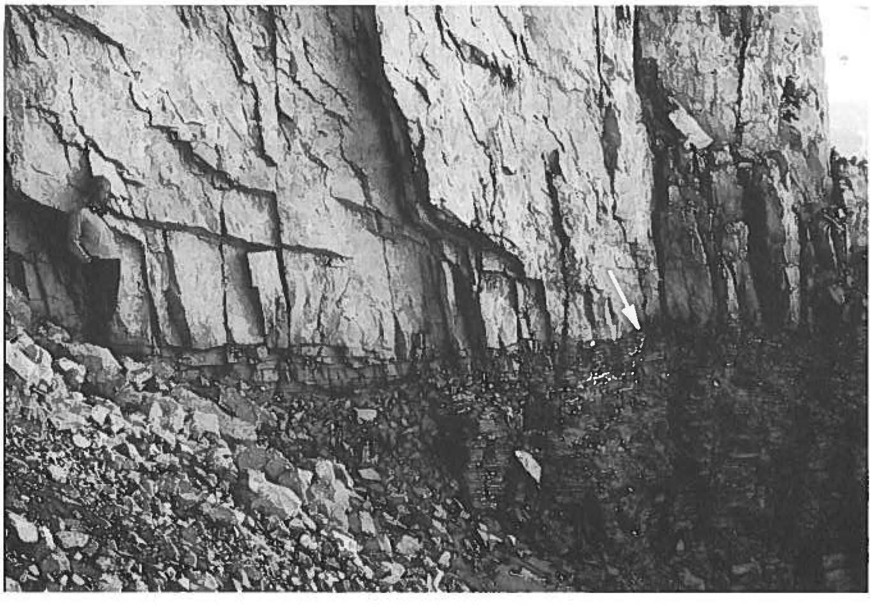

Fig. 9. Junction (arrowed) between the uppermost thin-bedded dolomites of the Holm Dal Formation and pale, cliff-forming dolomites (mass-flow breccias) of the overlying Perssuaq Gletscher Formation. Type locality of the Holm Dal Formation.

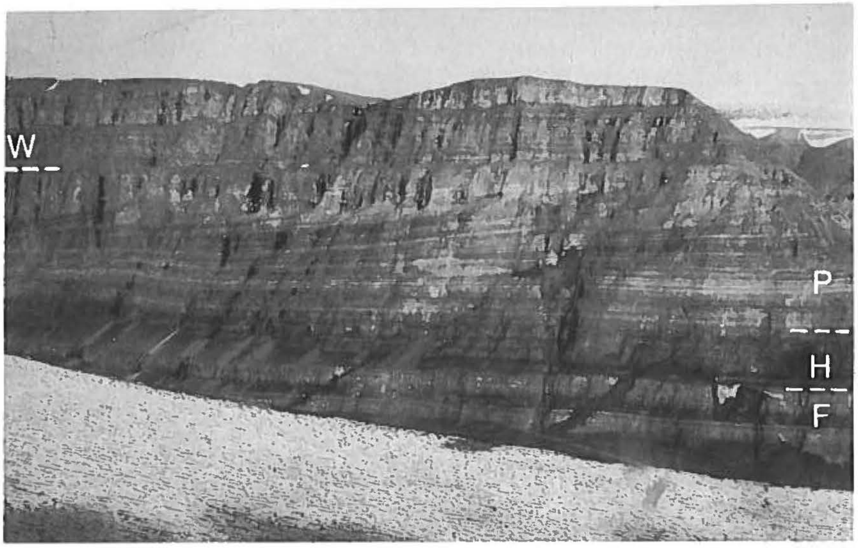

Fig. 10. Tavsens Iskappe Group on the east side of inner J. P. Koch Fjord. F: Fimbuldal Formation; H: Holm Dal Formation; P: Perssuaq Gletscher Formation; W: Wandel Valley Formation. Note the interdigitation of pale and dark strata within the lower Perssuaq Gletscher Formation, and the northward progradation of the pale facies.

Towards the top of the formation, dolomitised representatives of this facies show small-scale slumping and pull-apart structures.

Interpretation. – The widespread bioturbation and the presence of a trilobite-brachiopod fauna indicate an oxygenated open-marine environment. Sedimentary structures are not preserved but the alternation of mud-rich carbonates and lime silts or fine sands suggests an environment periodically winnowed by gentle bottom currents; deposition at or just beneath normal wave base is envisaged.

Handford (1986) described similar muddy peloidal lime sands from the Carboniferous of Arkansas which he attributed to deposition at moderate depths (15–30 m) on a storm-dominated shelf. The possibility of storm influence cannot be ascertained in this bioturbated facies.

Lithofacies 5, sandstone

Pale fawn or brown, fine-grained dolomitic sandstones form a small proportion (5 %) of the Holm Dal Formation; siliciclastic deposits are more typical of the overlying Perssuaq Gletscher Formation (see Surlyk & Ineson 1987). They occur in the upper levels of the Holm Dal Formation in its type section and characteristically show thin, flaggy bedding. Parallel lamination and ripple cross-lamination were recorded although bioturbation commonly obscures depositional structures; the trace fossil *Multipodichnus* has been described from this facies (Bergström & Ineson, this volume).

Interpretation. – Parallel and cross-lamination indicate deposition from tractional bottom currents. The siliciclastic sand was probably introduced into the carbonate-dominated environment by offshore storm-surge currents (the 'punctuated mixing' of Mount 1984).

Lithofacies 6, carbonate breccias

Limestone and dolomite breccia beds range in thickness from 0.1 to 6 m; the thicker beds generally occur near the base of the formation (Fig. 7). These thicker beds (>1 m) are laterally persistent sheets with flat, non-erosional bases and flat or hummocky tops. Thinner beds often pinch and swell, however, and can be lat-

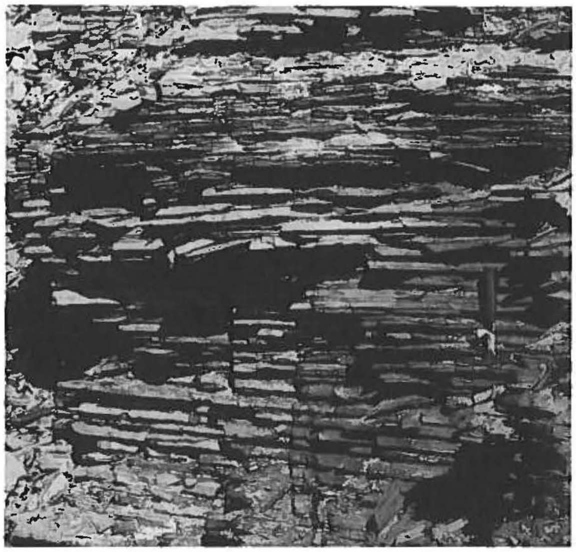

Fig. 11. Thinly-bedded argillaceous lime mudstones (Lithofacies 2). Note the regular alternation of limestone and shale and the flat, parallel bedding planes. Hammer (centre right) for scale.

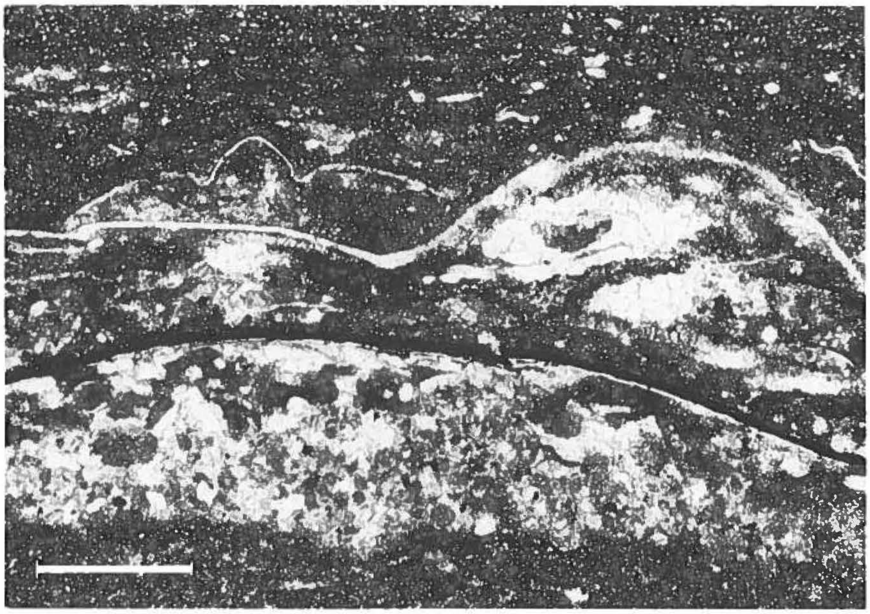

Fig. 12. Photomicrograph of laminated lime mudstone (Lithofacies 2) with thin silty laminae of peloidal skeletal packstone or grainstone. Skeletal elements are mainly trilobite. Scale bar = 0.5 mm.

erally discontinuous (Fig. 13), locally grading laterally into slumped but essentially in situ strata.

The breccias are clast-supported and largely ungraded. Although predominantly disorganised some beds show a preferred orientation of large flat clasts, parallel to bedding. Clasts are typically flat and tabular with an average long dimension of 5–20 cm, although slabs consisting of thin-bedded limestone may reach several metres in length. Such large slabs are often internally slump-folded. A few beds show a lower portion mainly composed of large contorted slabs, grading up into disaggregated pebble-cobble grade breccia.

Where undolomitised, the clasts are composed of slabs and fragments of parallel or wavy-bedded lime mudstones, packstones and grainstones comparable to Lithofacies 2 and 4; the interstitial matrix is typically argillaceous lime mudstone but quartz sandstone matrices were recorded near the top of the formation. Several breccia beds are capped by a graded peloidal lime grainstone bed, up to 50 cm thick, showing parallel and ripple cross-lamination.

Interpretation. – These chaotic, poorly sorted muddy breccias are interpreted as viscous debris flow deposits (Ineson 1980; see also Johnson 1970; Lowe 1979; Hiscott & James 1985). The outsized 'floating' slabs and hummocky upper surfaces attest to the cohesive and frictional strength of the debris. Grainstone caps on

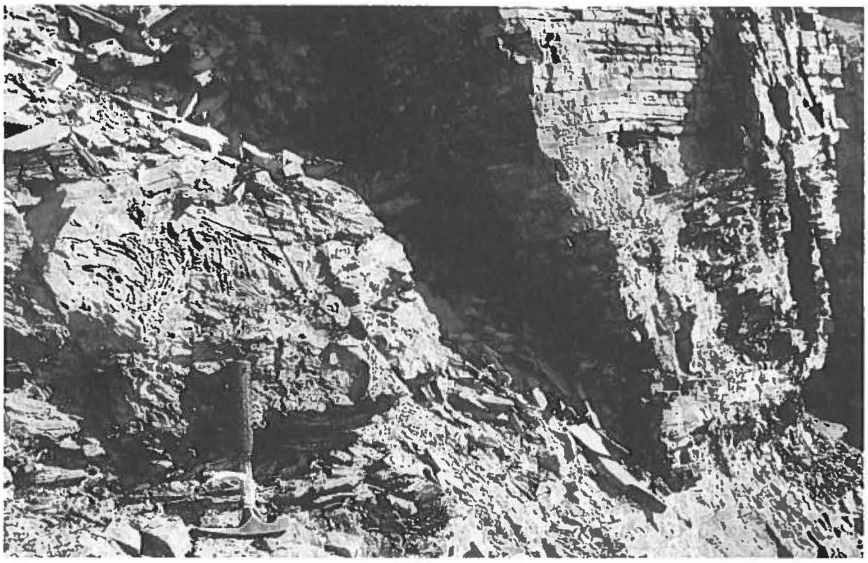

Fig. 13. Thin limestone breccia bed (Lithofacies 6) pinching out laterally (arrow) within thin-bedded lime mudstones. Note the clast-supported chaotic internal structure of the mass-flow breccia bed.

these debris flow deposits are attributed to turbidity currents associated with these viscous mass flows (Ineson 1980; see Krause & Oldershaw 1979).

Local derivation of the mass flows is suggested firstly by the close lithological match between clasts and enclosing strata and the lack of blocks of shallow-water origin, as seen elsewhere in the succession, for example in the underlying Fimbuldal Formation (see discussion below). Secondly, several thin breccia beds grade laterally into slumped, partially disaggregated strata. Atypical in this respect is the uppermost breccia bed in the type section, which has a medium-grained quartz sand matrix and clearly was derived from outside the immediate environment.

Facies distribution

The distribution of Lithofacies 1–6 in the type section is shown schematically in Fig. 14. Carbonate breccia beds (Lithofacies 6) occur sporadically throughout but the remaining facies show a systematic upward change. Silty, laminated bituminous carbonates (Lithofacies 1) occupy much of the basal 20 m; the phosphorite hardground (Lithofacies 3) occurs within this lower unit. Argillaceous lime mudstones (Lithofacies 2) dominate the middle two-thirds of the section; skeletal grainstone laminae appear in this lithofacies at about 40 m above the base of the formation and are most abundant between 70 and 80 m. Burrowed peloidal grainstones, packstones and wackestones (Lithofacies 4) form much of the upper 50 m, with occasional thin sandstone interbeds.

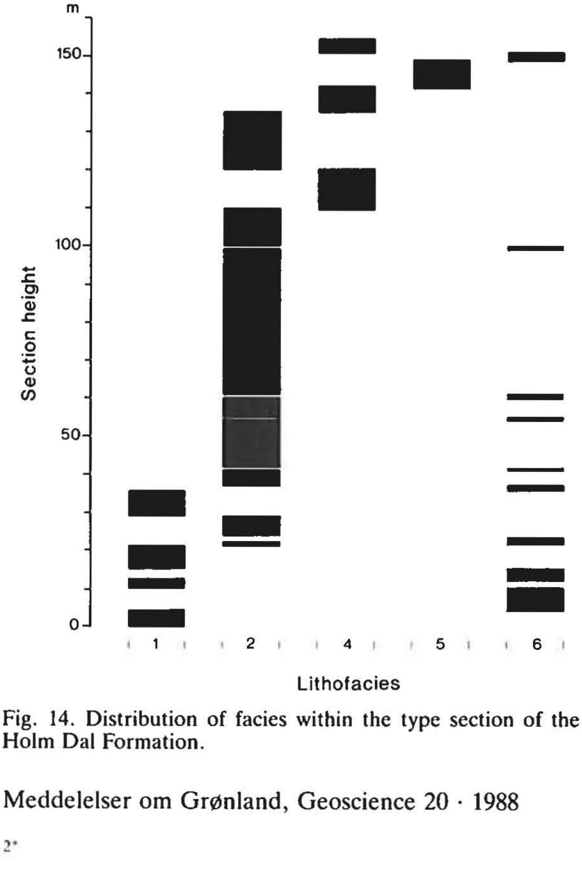

Fig. 14. Distribution of facies within the type section of the Holm Dal Formation.

Although mass-flow deposits occur at intervals throughout the formation, the thicker more extensive deposits occur within the basal 25 m, and small-scale evidence of downslope movement (minor slump folds, pull-aparts) is most common within the lower and uppermost levels of the formation (Fig. 7). Mass-flow breccias are thin and laterally discontinuous in the intervening central portion of the formation.

A similar facies trend occurs in the Holm Dal Formation in the Navarana Fjord area (Fig. 1) where bituminous, laminated dolomites forming the basal 25 m are succeeded by thin-bedded argillaceous lime mudstones with skeletal grainstone laminae (J. S. Peel, pers. comm. 1986). At the top of the formation, dolomitic argillaceous lime mudstones are overlain by bioturbated fine sandstones of the Perssuaq Gletscher Formation (Surlyk & Ineson 1987; Fig. 6).

Depositional environment

Considered in isolation from the underlying Fimbuldal Formation and overlying Perssuaq Gletscher Formation, the Holm Dal Formation records deposition in an open marine, mainly low-energy environment. Poor circulation commonly resulted in oxygen-deficient bottom waters. Carbonate and siliciclastic muds and silts accumulated mainly from suspension or, less commonly, from dilute density currents or storm currents. The mass-flow deposits and small-scale slope creep and slump structures reflect periodic slope instability in the immediate depositional area. The facies represented are closely comparable with those of 'open shelf' or 'deep shelf' environments (e.g. Wilson 1975); this broad depositional setting is compatible with that deduced from the trilobite assemblage (Robison, this volume).

The type section can be readily subdivided into three units, each reflecting stages in the progressive shallowing of the environment. The basal 20 m of bituminous, laminated silty carbonates, intercalated with mass-flow breccias, represent a period of sediment starvation; carbonate input was low and consequently siliciclastic silt and mud form an important component of the sediment column. The presence of phosphoritised pellets and locally a phosphorite-impregnated hardground, are further evidence of reduced sedimentation rates (Baturin 1982). The succeeding 80 m of argillaceous lime mudstones with rare, thin mass-flow breccia beds, represent an environment beneath normal wave base but periodically swept by weak bottom-currents. The upward increase in winnowed skeletal laminae reflects the progressive shallowing of the environment. The uppermost interval of fossiliferous peloidal grainstones, packstones and wackestones records shallowing to close to normal wave-base. Fine sandstones in this interval were probably introduced by offshore storm-induced currents and herald the northward progradation of shallow-marine sandstones forming the overlying Perssuaq Gletscher Formation.

Some discussion of the environmental implications of adjacent formations is needed to further this interpretation. The underlying Fimbuldal Formation consists of 180 m of platy nodular lime mudstones and dolomites interbedded with thick, laterally persistent carbonate breccia beds, locally containing blocks of ooid grainstone several tens of metres across. This sequence is interpreted as a suite of carbonate slope deposits (Ineson 1980, 1985). Coeval rocks farther south represent a northward-prograding platform margin fringed by ooid sand banks; the ooidal grainstone blocks within the Fimbuldal Formation mass-flow deposits were probably derived from the unstable outer margin of this advancing platform.

In complete contrast, the Holm Dal Formation is overlain by a mixed sequence of quartz arenites and carbonates assigned to the Perssuaq Gletscher Formation (*c.* 400 m). In its type section, the Perssuaq Gletscher Formation includes sandy dolomite mass-flow deposits but is dominated by bioturbated and trough cross-bedded sandstones. This sequence typically shows northward-dipping clinoforms and demonstrably progrades northwards, individual units wedging out into the underlying Holm Dal Formation (Fig. 10; Surlyk & Ineson 1987). South of Navarana Fjord, the sandstones are locally interbedded with stromatolitic dolomites forming low-relief thrombolite mounds up to 2 m in height (Surlyk & Ineson 1987). The shallow-marine siliciclastics of the Perssuaq Gletscher Formation are truncated upwards by an unconformity; they reflect the northward progradation of the shoreline accompanying progressive exposure of the platform (Higgins et al., in press).

Thus the depositional history of the shelf between the mid-Middle Cambrian and the Late Cambrian can be regarded in terms of two distinct stages (Fig. 15):

1. During the medial Middle Cambrian a shallow-water carbonate platform prograded northwards, flanked to the north by an accreting wedge of carbonate slope deposits (Fimbuldal Formation), grading out onto the deep-water, outer shelf (Fig. 15a).
2. The bituminous silty carbonates of the basal Holm Dal Formation abruptly overlie these slope deposits and represent the onset of a major regressive cycle during the late Middle and Late Cambrian (Fig. 15b, c). This initial period of slow sedimentation and carbonate starvation on the outer shelf recorded in the basal strata probably reflects a relative sea-level fall (cf. James & Mountjoy 1983), resulting in exposure of much of the platform and consequently a marked decline in carbonate production. Although drowning of a carbonate platform can produce a similar starved sequence in coeval deeper-water environments (James & Mountjoy 1983), the increase in siliciclastic detritus in the Holm Dal Formation and the subsequent regressive sedimentation pattern exhibited by the Holm Dal and Perssuaq Gletscher Formations favour the former interpretation. Thus, following a relative fall in sea-level, carbonate sedimentation was re-established on the vestigial platform and outer shelf; the latter may have closely resembled a carbonate ramp in the late Middle and Late Cambrian (Fig. 15b). The clinoforms in the Perssuaq Gletscher Formation and the mass-flow deposits in both the Holm Dal and Perssuaq Gletscher Formations reflect relief inherited from the previous phase of carbonate platform development (Fig. 15b, c).

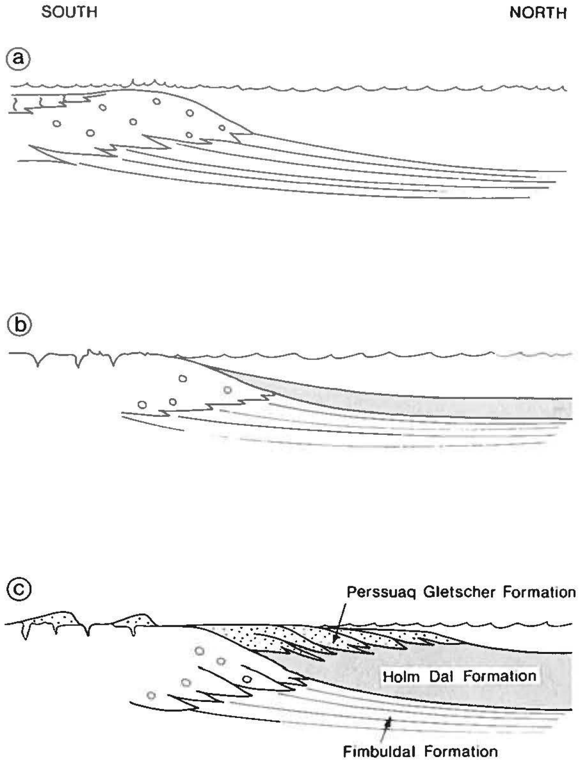

Fig. 15. Schematic cross sections illustrating the inferred evolution of the shelf during Middle-Late Cambrian. The sequence of events is described in the text.

The Holm Dal Formation thus forms the lower portion of a regressive cycle, probably initiated by a relative sea-level fall, and recording shallowing from starved deep-shelf into the shallow subtidal zone. Carbonate production was ultimately stifled by prograding littoral clastics heralding the exposure of the platform (Fig. 15c).

Acknowledgements

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

RICHARD A. ROBISON

Robison, R. A. Trilobites of the Holm Dal Formation (late Middle Cambrian), central North Greenland. Meddr Grønland, Geosci. 20: 23–103. Copenhagen 1988-12-31.

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.

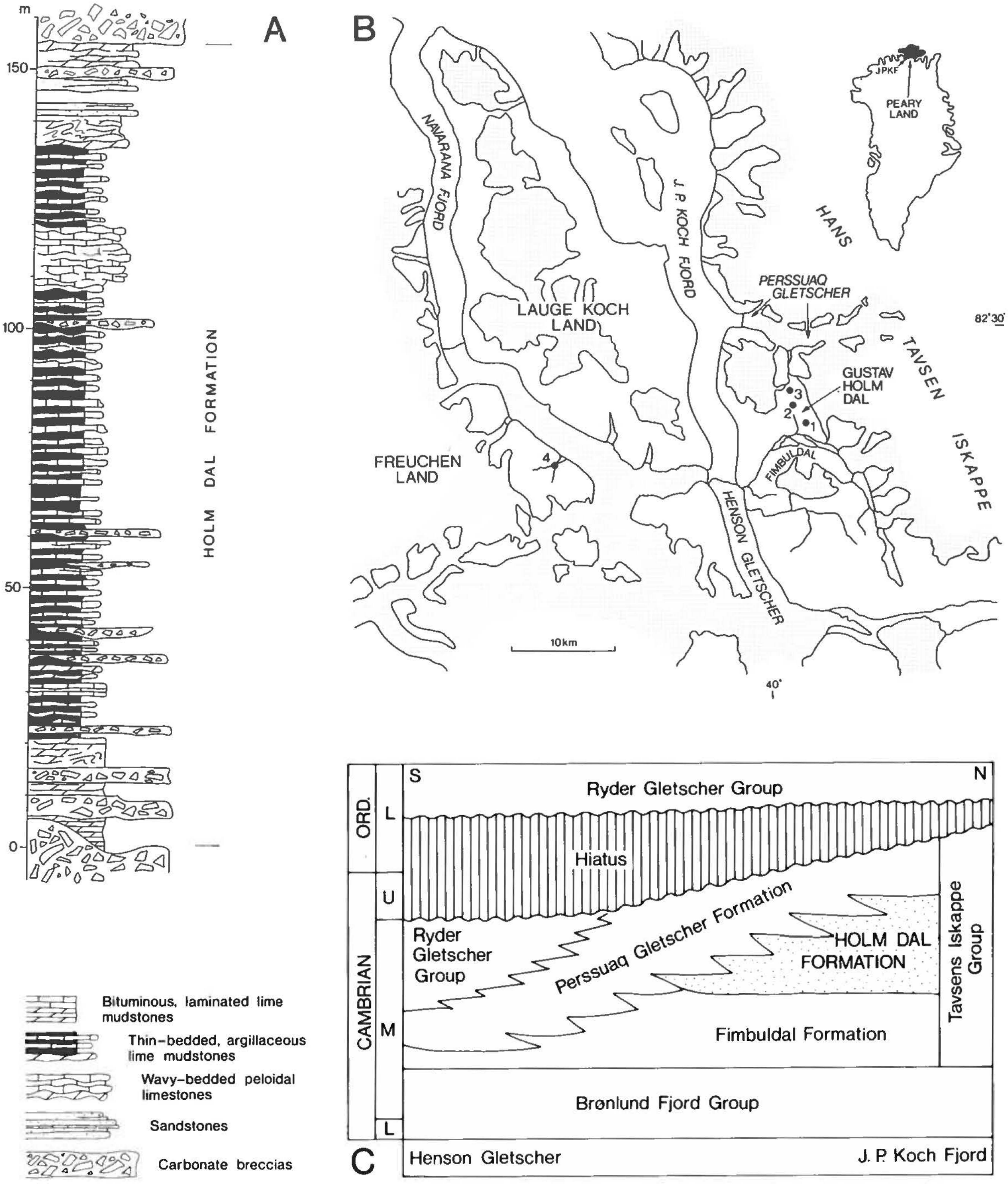


Fig. 1. Derivation of trilobites from the Holm Dal Formation, central North Greenland. A, stratigraphic section through the Holm Dal Formation at its type locality (locality 1 in Fig. 1B; from Ineson, this volume). B, map of the area around Gustav Holm Dal, westernmost Peary Land, central North Greenland. 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).

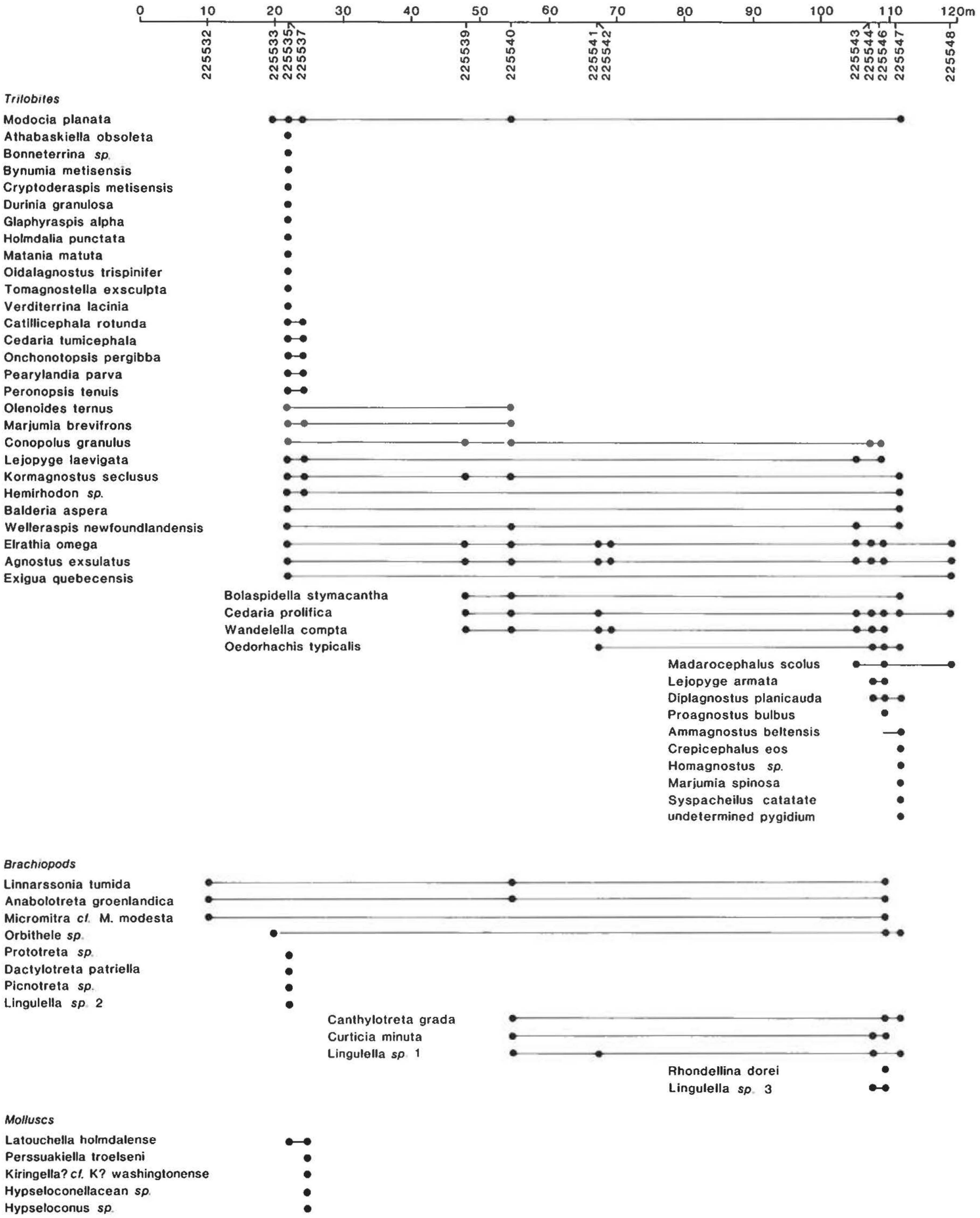


Fig. 2. Stratigraphic distribution of trilobites, brachiopods, and molluscs described from the type section of the Holm Dal Formation (locality 1, Fig. 1B). Six-digit numbers designate GGU collections. The formation is almost 155 metres thick in its type section (Fig. 1A); scale indicates height above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

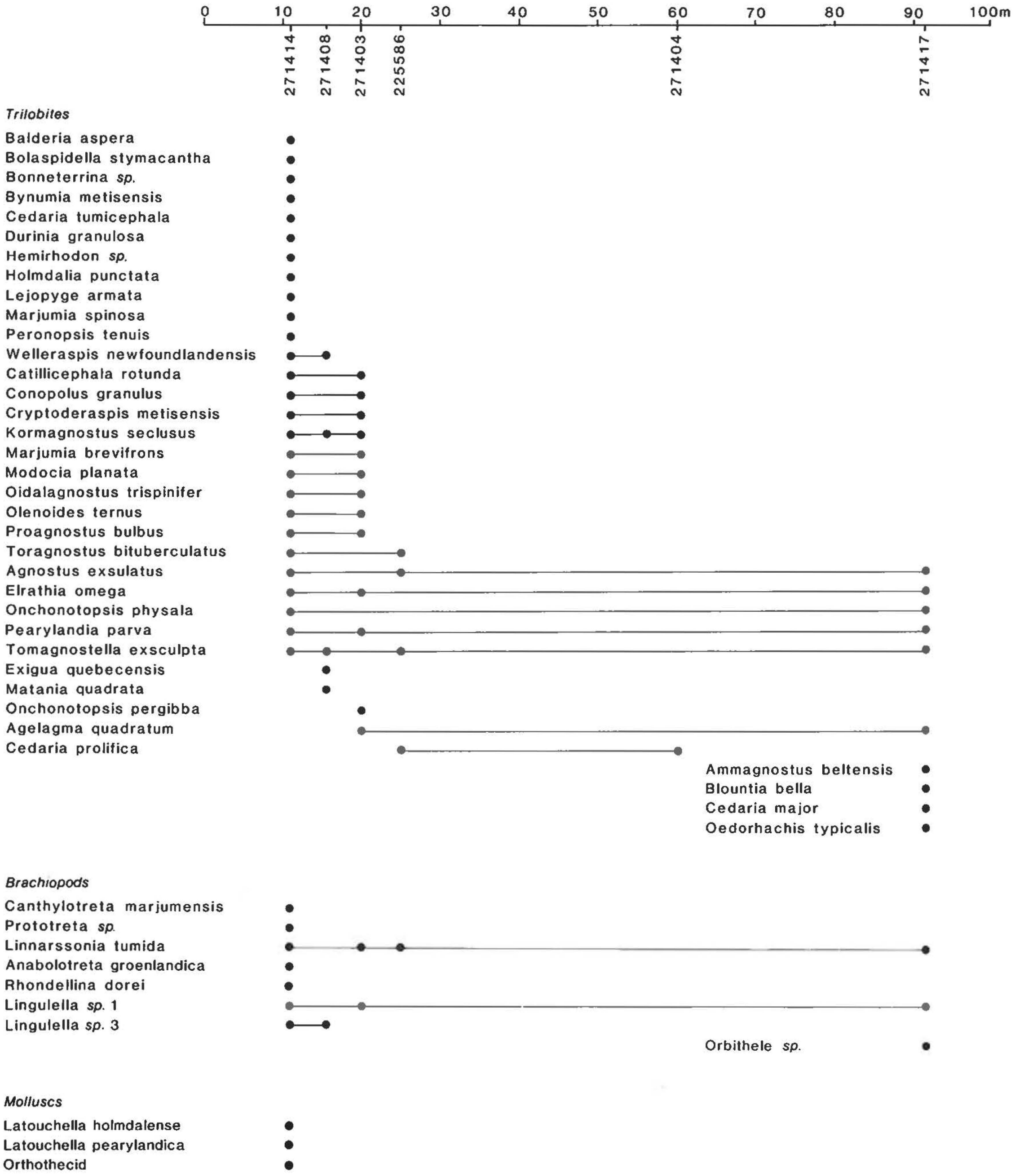


Fig. 4. Stratigraphic distribution of trilobites, brachiopods, and molluscs described from locality 2 (Fig. 1B) of the Holm Dal Formation. Six-digit numbers designate GGU collections. Scale indicates height above base of formation.

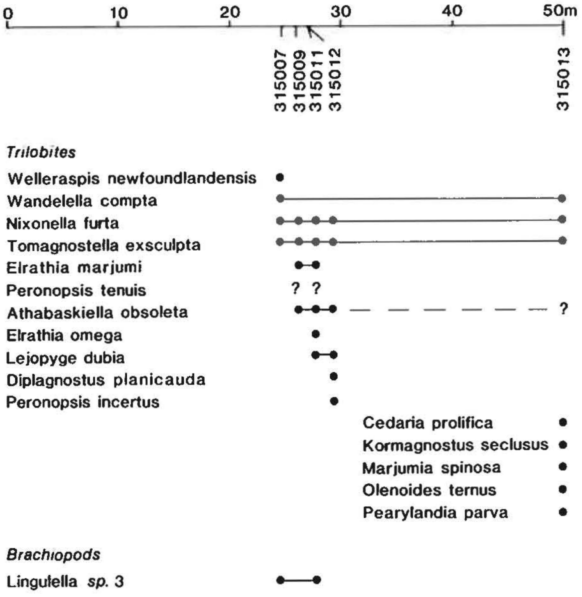


Fig. 6. Stratigraphic distribution of trilobites and brachiopods in GGU collections from locality 4 (Fig. 1B) of the Holm Dal Formation in south-east Freuchen Land. Scale indicates height above the base of the formation.

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.

	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.

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.

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

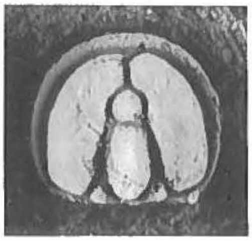
Genus *Diplagnostus* Jaekel 1909

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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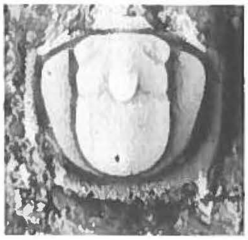
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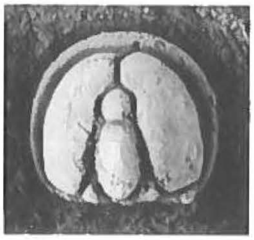

1b


2b


3b


1c

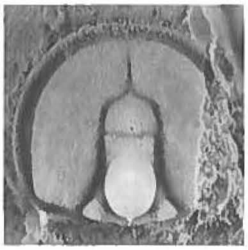

2c


6


3a


4a


5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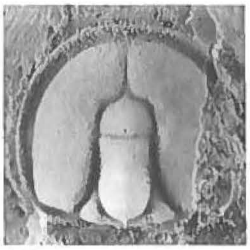
8a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8b


7c


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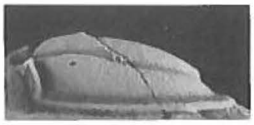
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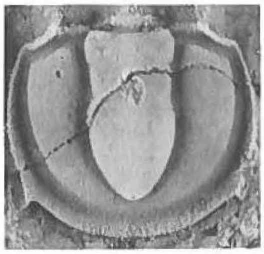
4b


9


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.


1a


2


1b


3


4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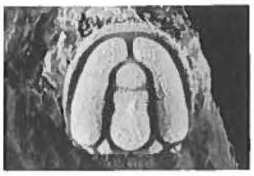
6


7


9


10


14c


8


11c


15c


11a


12


11b


13


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*.

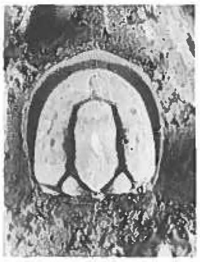
Oidalagnostus and *Dolichagnostus* Pokrovskaya 1958, appear to be closely related. *D. admirabilis* Pokrovskaya 1958, the type species of *Dolichagnostus*, lacks a pygidial collar but closely resembles *O. debori* (Jago 1976) in axial structure.

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.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2a


3


2b


2c


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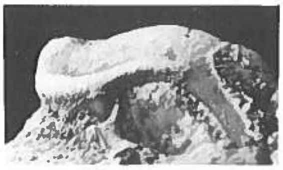
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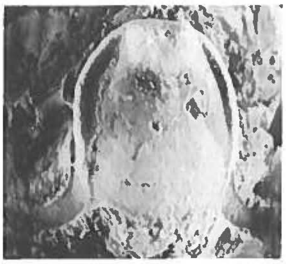
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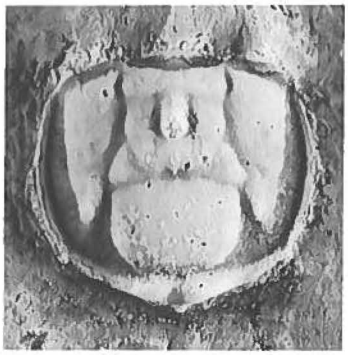
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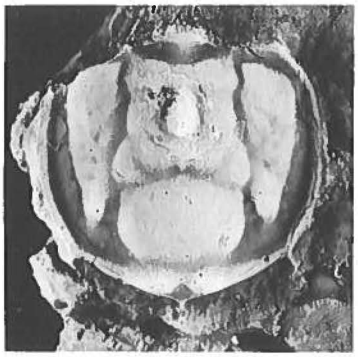

11

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.

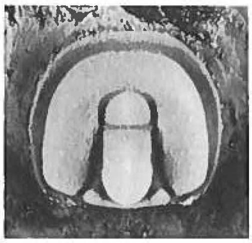
Occurrence. – *A. beltensis* is known from Argentina, Greenland, and the United States. Its observed stratigraphic range seems to be confined to the *Lejopyge laevigata* Zone. In Greenland, it is present in lime mudstone, packstone, and grainstone through the lower 111 m of the Holm Dal Formation.

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.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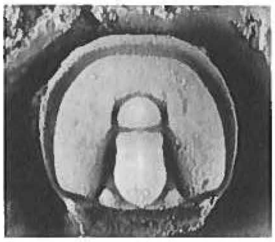
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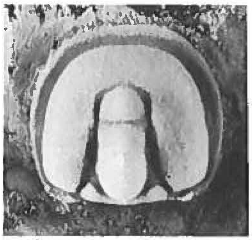
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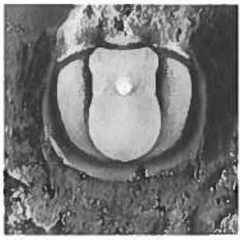
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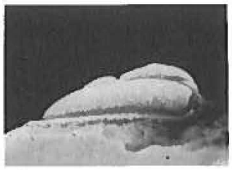
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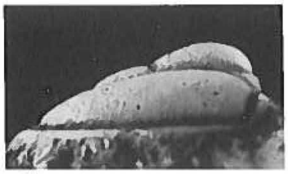
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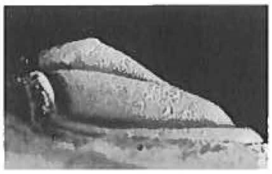
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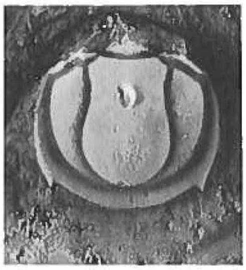
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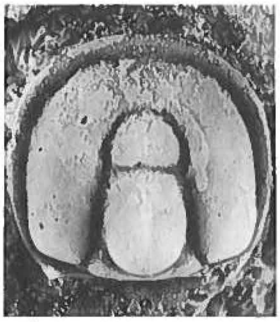
6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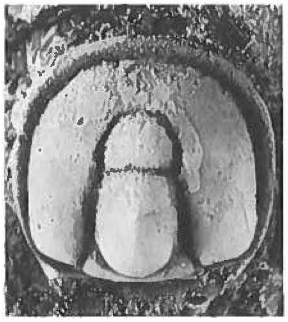
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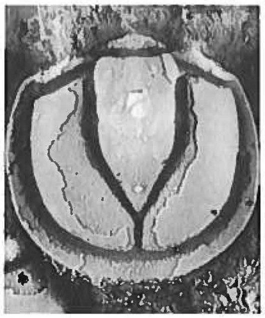
9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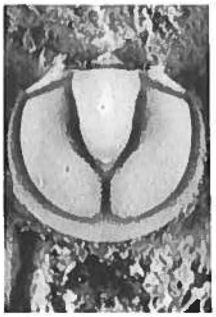
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10b


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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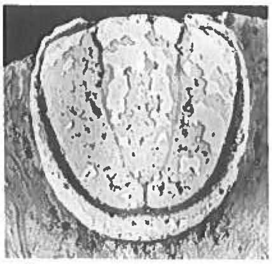
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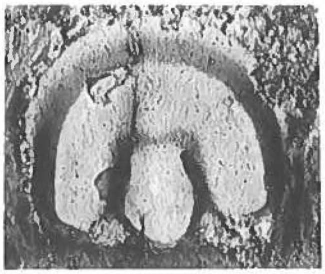
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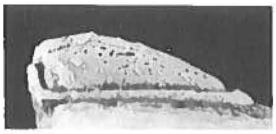
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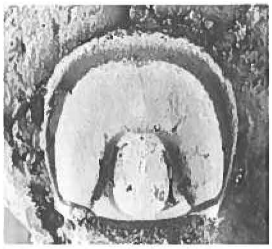
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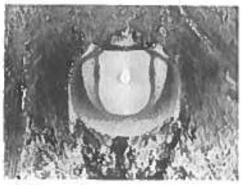
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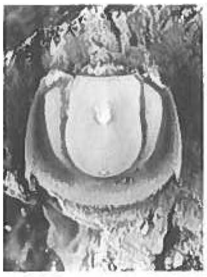
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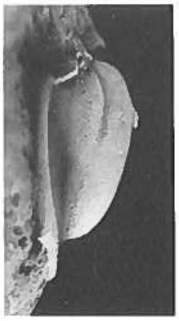
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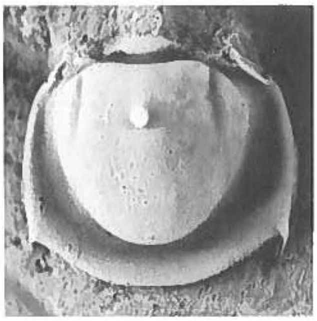
15b

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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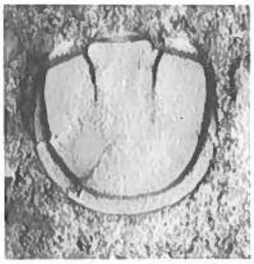
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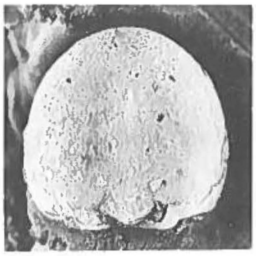
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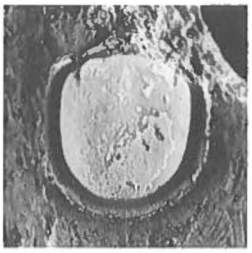
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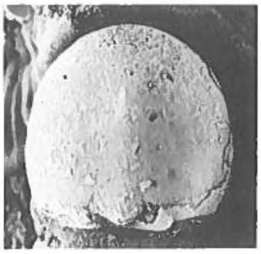
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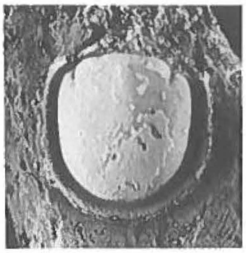
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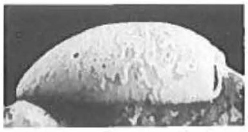
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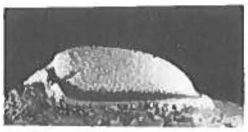
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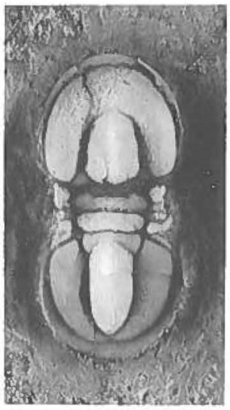
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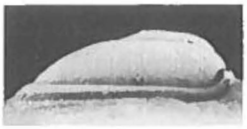
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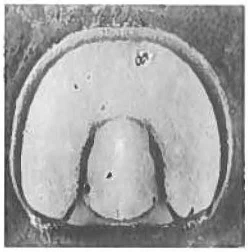
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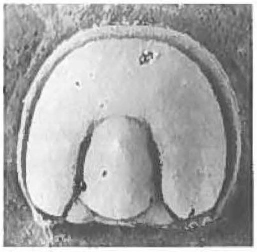
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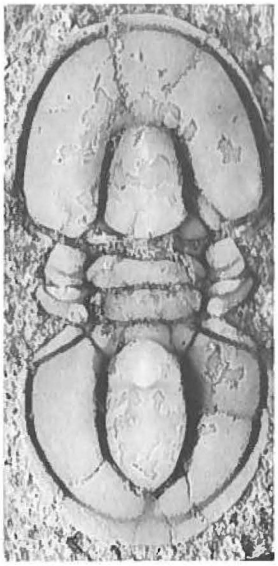
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Genus *Tomagnostella* Kobayashi 1939a

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.

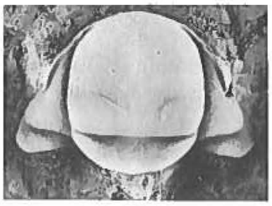
Blountia sp. 2

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.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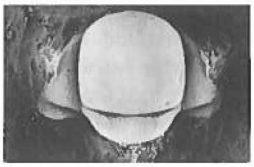
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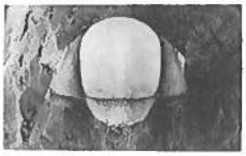
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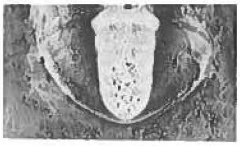
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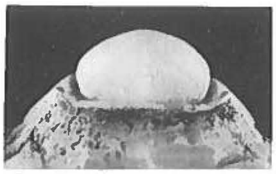
4b


2b


1b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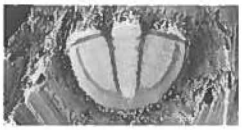
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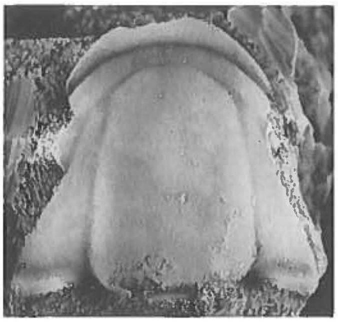
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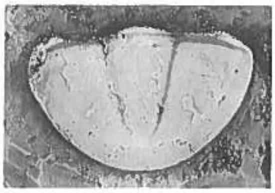
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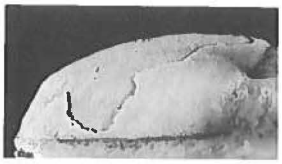
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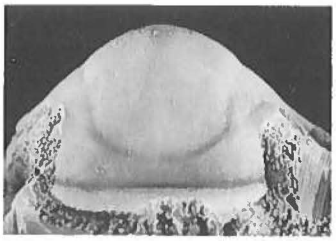
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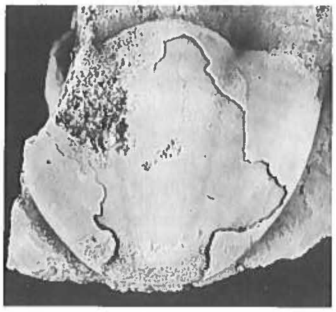
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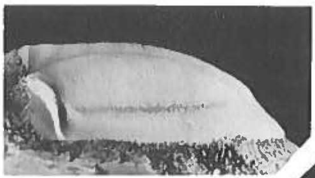
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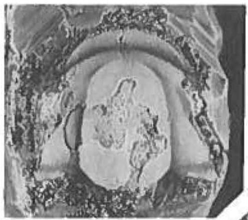
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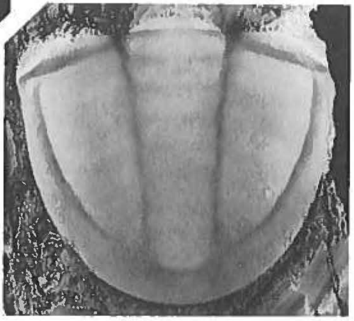
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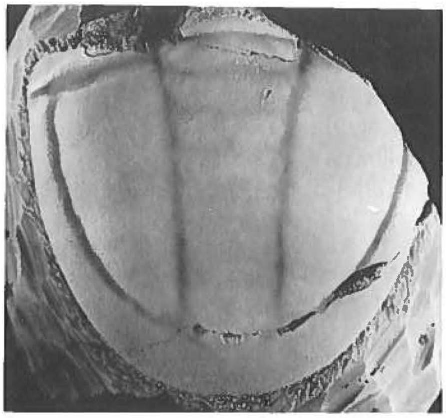

12

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.

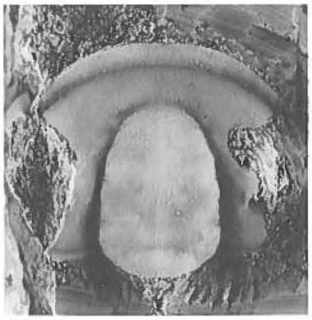
Diagnosis. – Cranidial axis moderately large. Occipital furrow nearly effaced. Palpebral area of fixigena horizontal or slightly upsloping. Pygidium having poorly defined border of moderate width; segmental features weak anteriorly, becoming effaced posteriorly.

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.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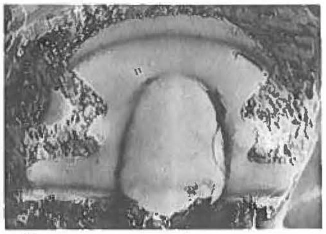
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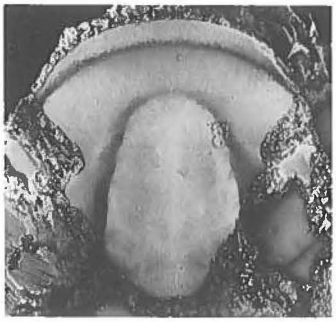
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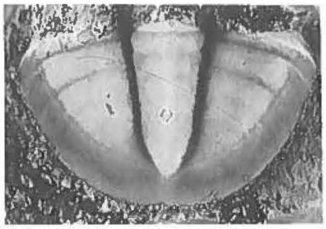
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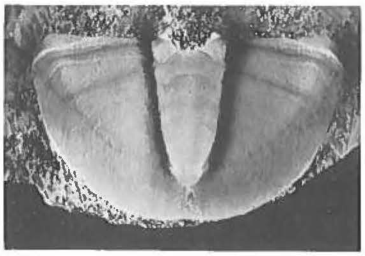
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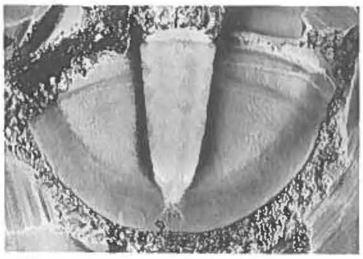
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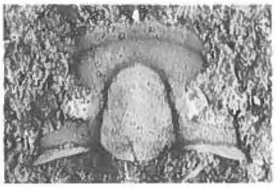
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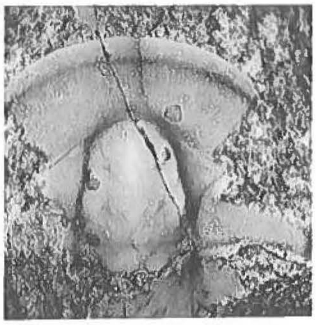
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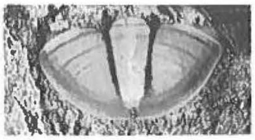
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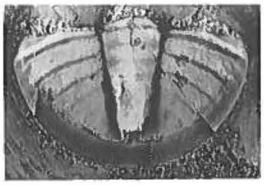
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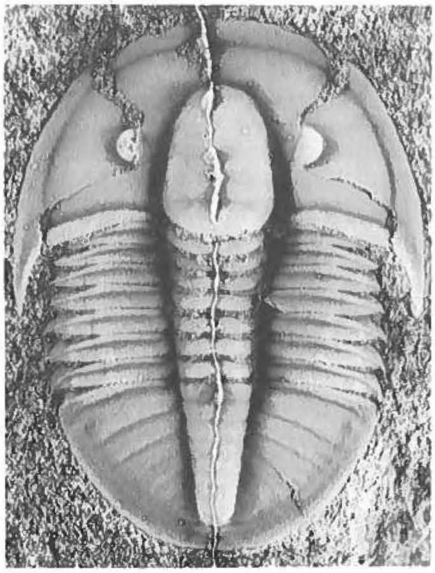
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Occurrence. – *C. major* is abundant in a dolomitized trilobite packstone from about 93 m above the base of the Holm Dal Formation. A predominance of large sclerites suggests significant winnowing or current sorting during predepositional transport. 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

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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.

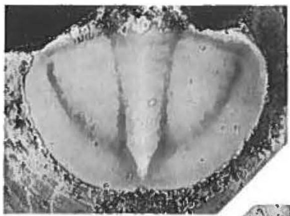
6–10. *Crepicephalus eos* n. sp., all X 4.4. 6. Anterior fragment of mostly exfoliated, smaller holaspid cranidium, MGUH 17.208 from GGU 225529. 7. Larger cranidium showing pitted anterior border furrow and vascular prosopon on preglabellar field, MGUH 17.209 from GGU 225547. 8. Mostly exfoliated cranidium 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.


1


2a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2b


2c


5a


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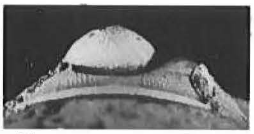
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8c


8a


5b


3b


9a


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9b


11a

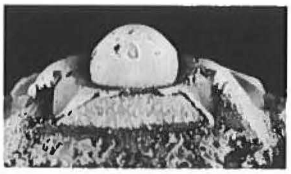

12a


13a


14


11b


12b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13b


15

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

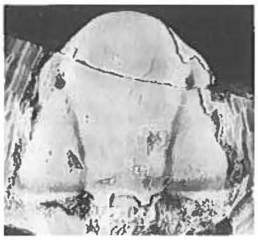
New material. – Two cranidia, two pygidia, a questionably assigned labrum, and a few questionably assigned thoracic segments in GGU 225535, 315009, 315011, 315012, and ?315013.

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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1b


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4b


8a


1c


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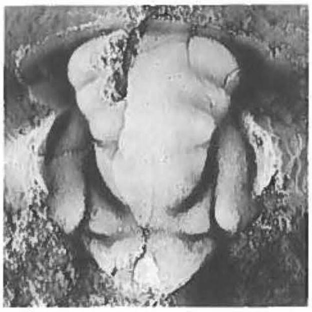
8c


10a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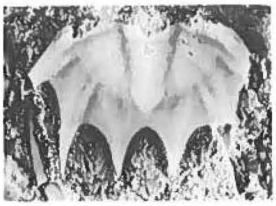
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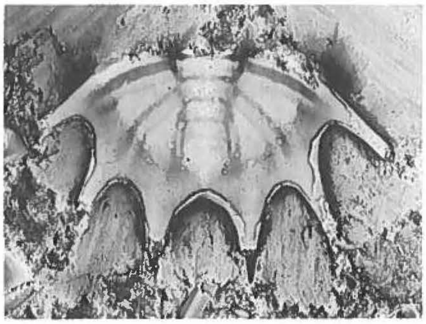
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Family Dorypygidae Kobayashi

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

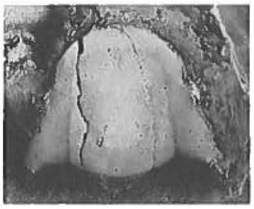
Kingstonia peltata – Palmer in Palmer & Peel 1981: 25, pl. 4: 1–11, 13, 14

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-


1a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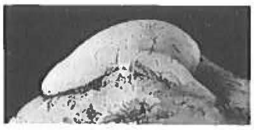
1b


2b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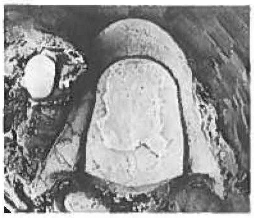
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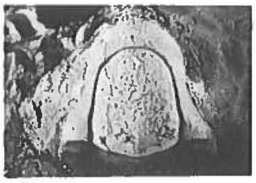
4


1d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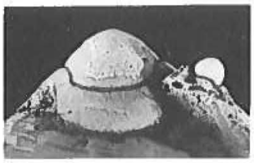
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7


6


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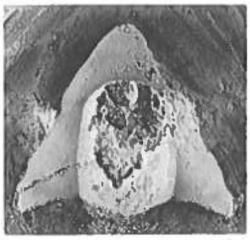
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10


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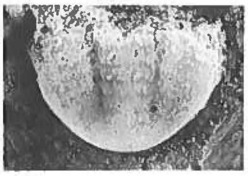
14b


9b


13a


11b


14a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13b


13c

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.

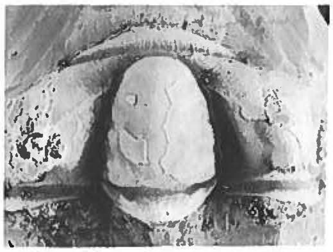
Although previously unreported, rare specimens of *A. quadratum* have been collected from the uppermost bed of the medial limestone marker unit of the Lincoln Peak Formation in the southern White Pine Range, about 4 km north-east of Currant, Nye County, Nevada (R. A. Robison collection 795). A cranidium 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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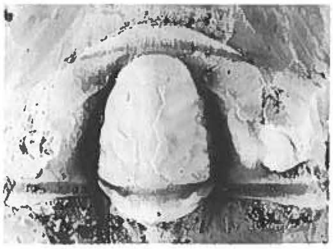
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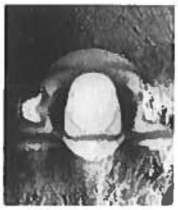
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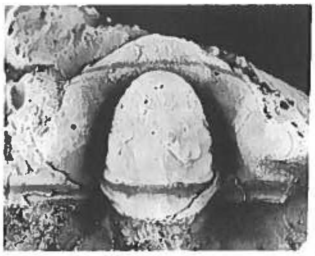
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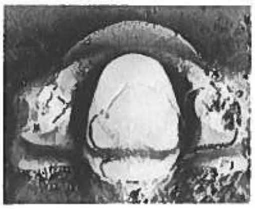
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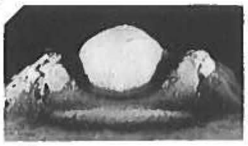
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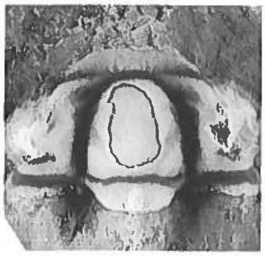
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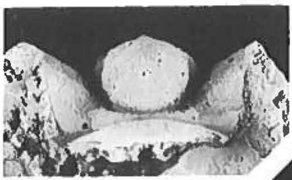
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10


4c


11


12a


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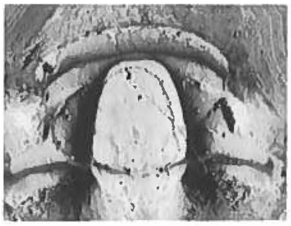
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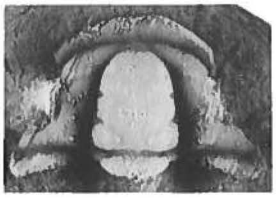
15a


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16


14b


14c


15b

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.


1a


2a

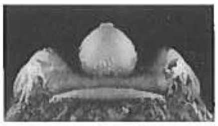

1b


2b


3a

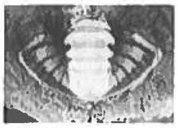

3b


4

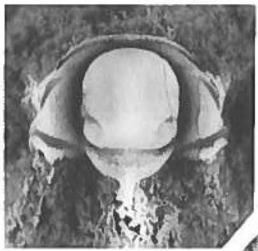

1c


1d


3c


5a


5b


6a


7

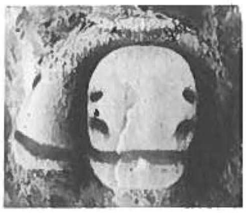

9b

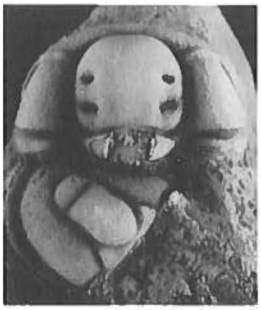

8


10

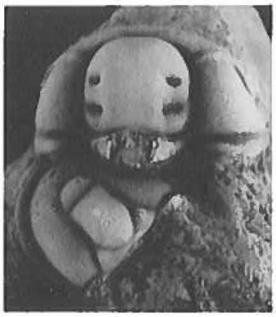

6b


9a


11a


12a


11b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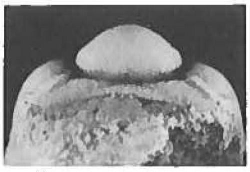

12c


13


12d


14a


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.

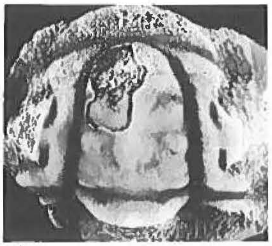
Cephalic surface finely granulose except in furrows and on muscle scars. Pygidial surface finely pitted and with fine granules on marginal areas. Terrace lines sparse and weak around cephalic and pygidial margins.

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*.

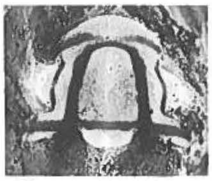
M. brevifrons differs from *M. typa* by having a shorter preglabellar field, a posteromedial expansion of the anterior cranidial border, and one rather than three pairs of spines on the pygidial border.

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.


1a

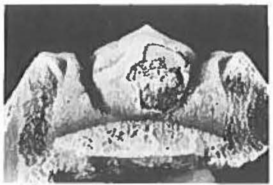

2a


3


4


2b


5


1b


6

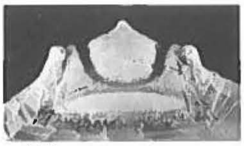

7


8


9a


1c


10a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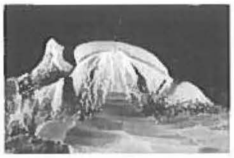
9b


9c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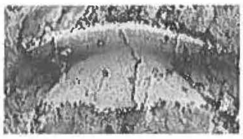
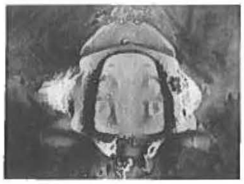

11


12b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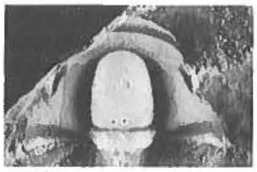
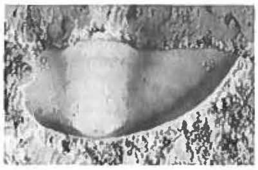

14


13a


13b


15a


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.

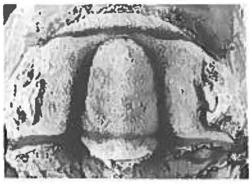
Material. – Four cranidia and four pygidia in GGU 225547, 225552, 225561, and 225564.

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.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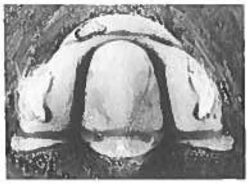
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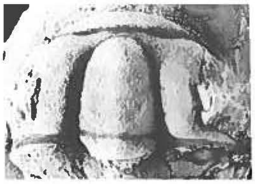
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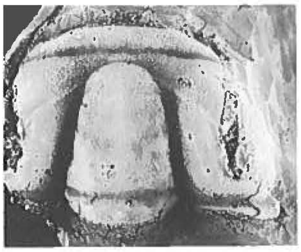
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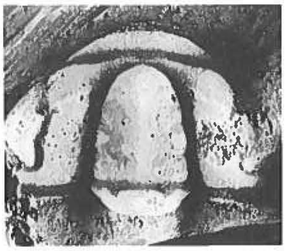
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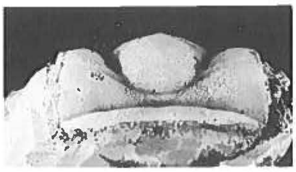
3b


3c


4c


6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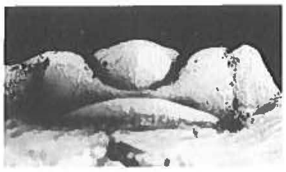
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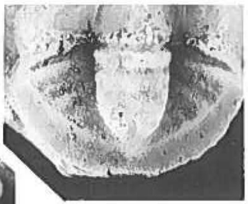
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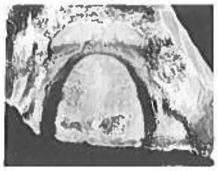
11a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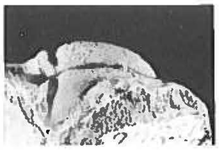
11b


12b


11c


13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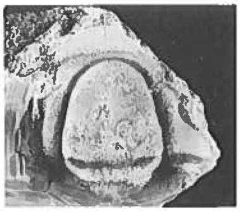
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12c

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.

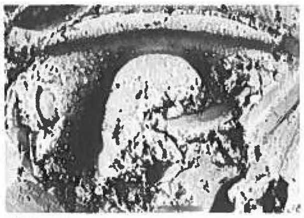
Diagnosis. – *Bolaspidella* having an erect occipital spine, moderately tapered glabella, palpebral lobe anterior from glabellar midpoint, and subequally divided frontal area.

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.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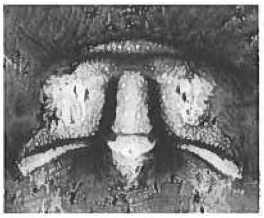
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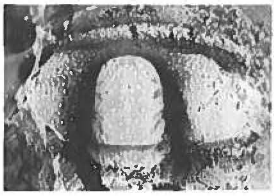
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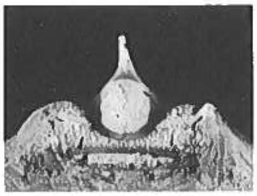
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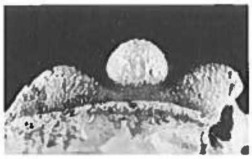
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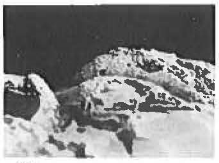
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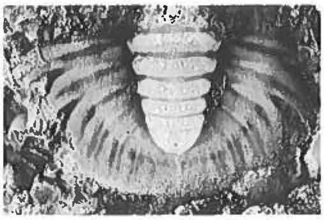
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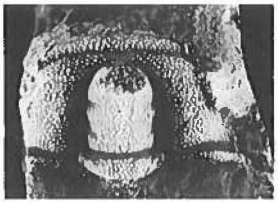
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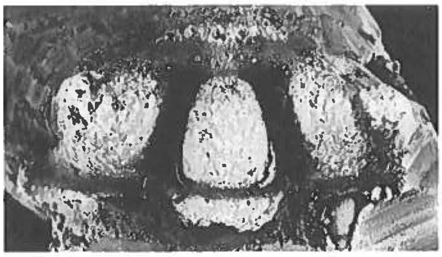
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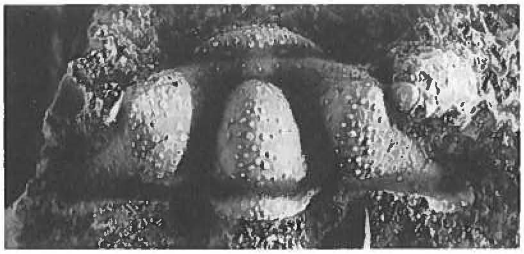
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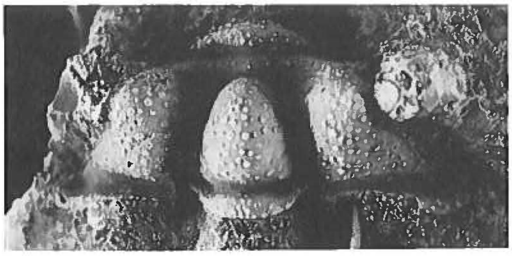
12b

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.


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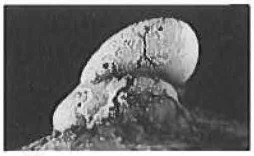
2a


1b


3a


1c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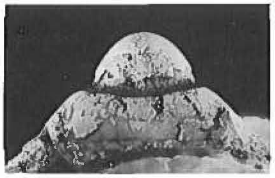
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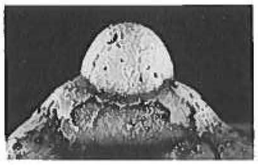
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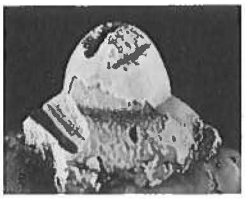
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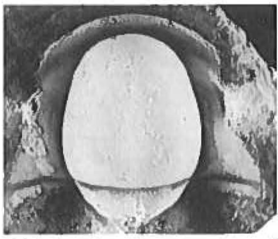
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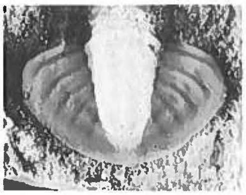
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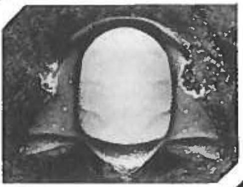
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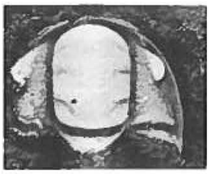
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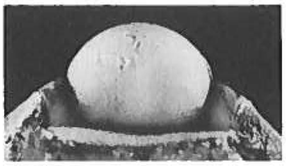
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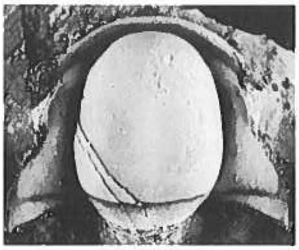
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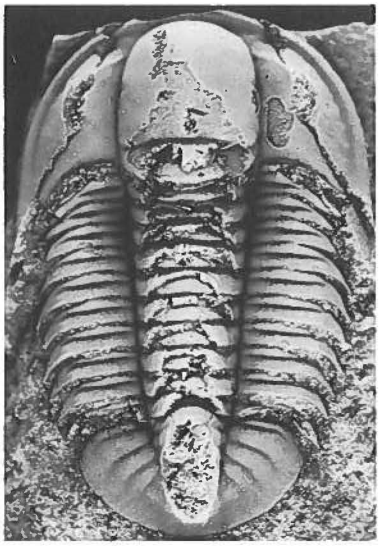
11b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Diagnosis. – *Durinia* of small size; largest observed cranidium about 3 mm long, exclusive of occipital spine, but most cranidia are less than 2 mm long. Glabella subrectangular in smaller specimens, becoming ovoid in largest specimens. Preglabellar 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.

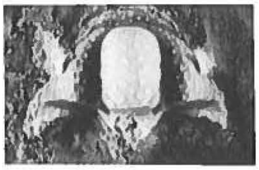
?Family Solenopleuridae Angelin

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


1a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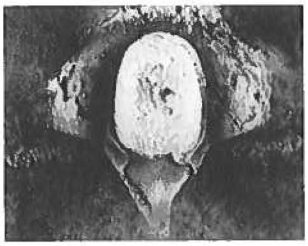
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1b


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6d


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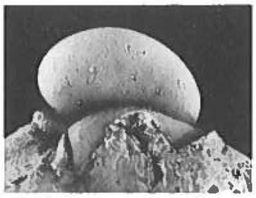
10b


11c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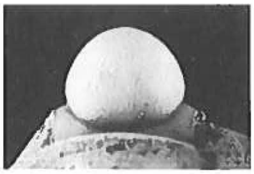
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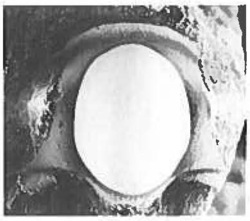
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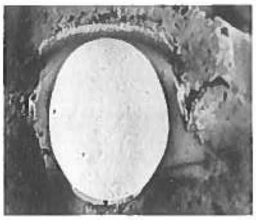
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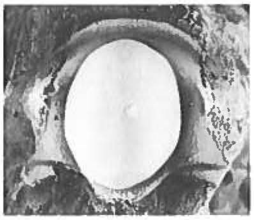
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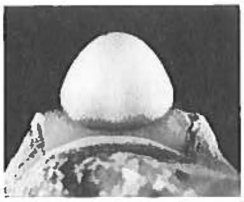
12c

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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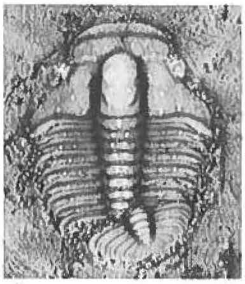

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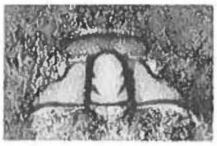

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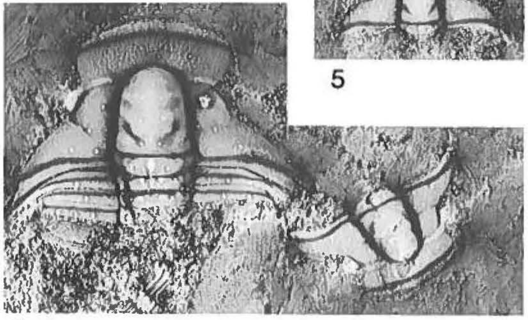

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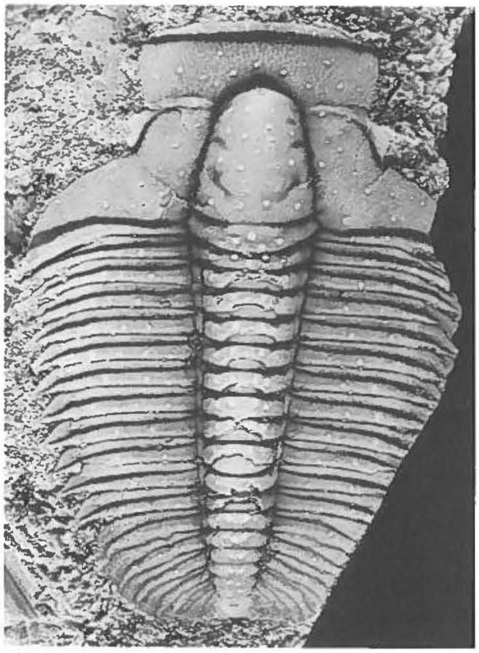

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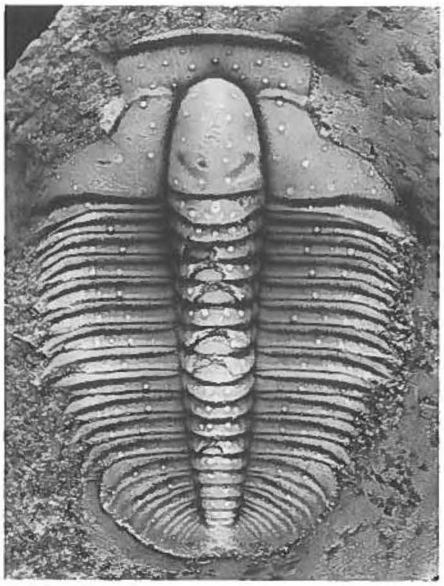

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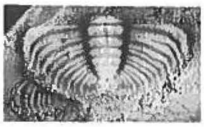

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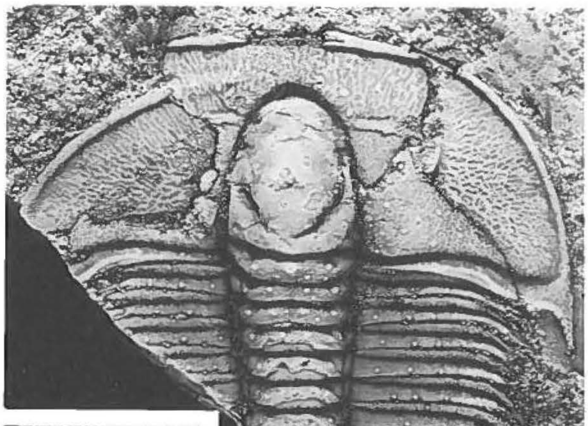

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Family uncertain

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.

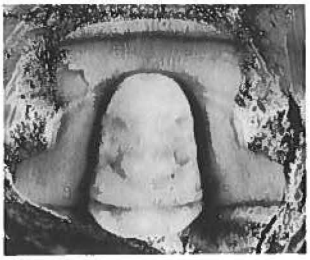
Material. – Several dorsal exoskeletons and many disarticulated sclerites in GGU 225529, 225535, 225539–225544, 225546, 225548, 225561, 225563, 225592–225595, 271403, 271414, 271417, and 315011.

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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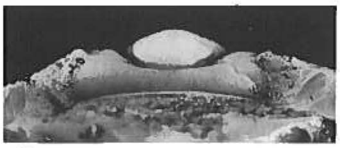
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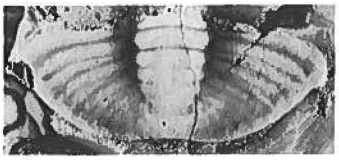
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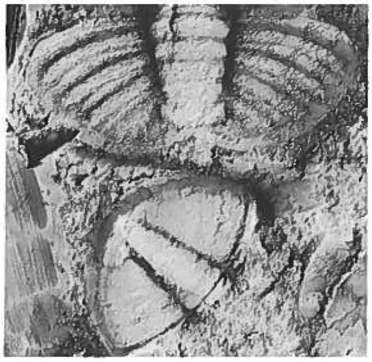
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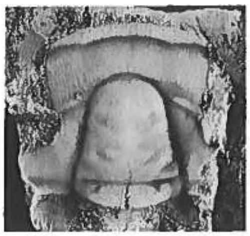
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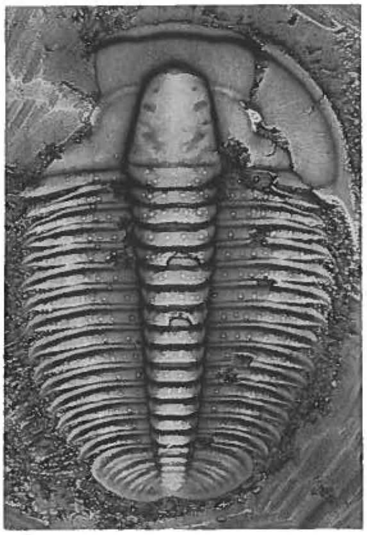
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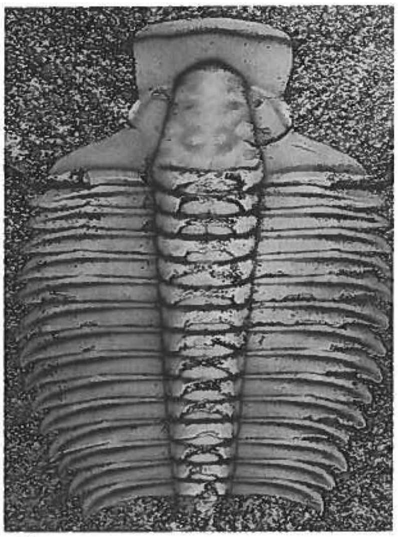
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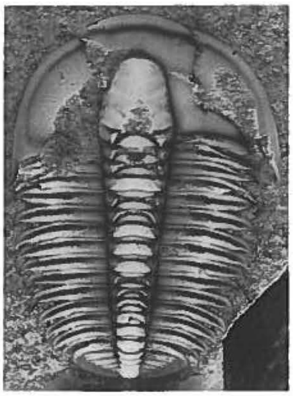
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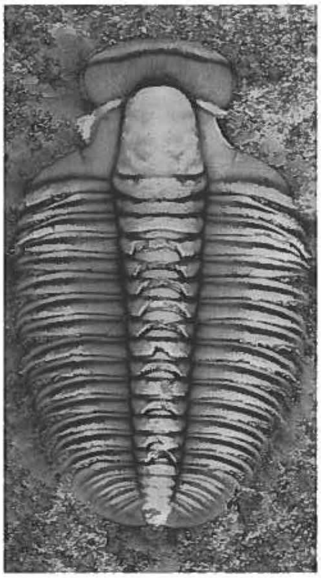
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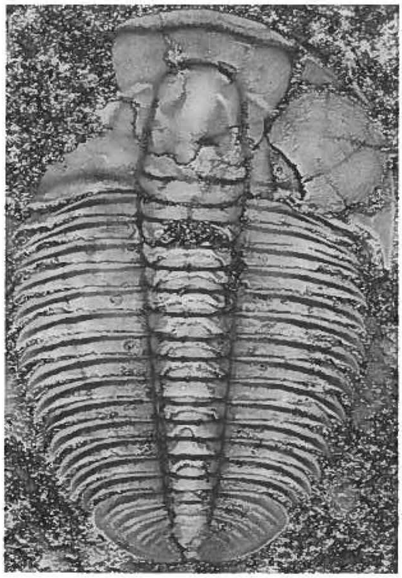
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ring having weak medial node. Eye ridge generally well developed, confluent with short palpebral lobe. Genal spine moderate in length, terminating near end of fourth thoracic segment. Thorax with 14 segments. Pygidium alate; anterolateral margins may 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.

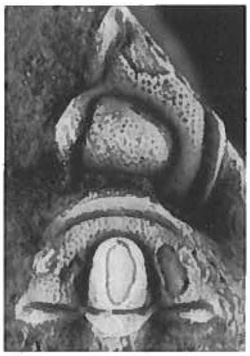
Remarks. – Two cranidia, one immature, can not readily be assigned to any trilobite genus. Because of the distinctive combination of characters listed in the diagnosis, I assign these specimens to *Verditerrina* n. gen. In glabellar form, *Verditerrina* resembles such Middle Cambrian genera as *Bolaspidella* 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.

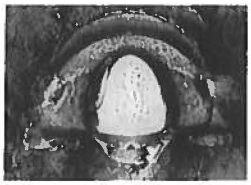
6–10. *Conopolus granulus* n. gen. and n. sp. 6, 9, 10. Pygidia of decreasing size, which are questionably assigned to this species; MGUH 17.373–17.375 from GGU 271414, 225552, and 271414 respectively, all X 6.6. 7. Holotype cranidium in stereo (a, b), frontal (c), and left-lateral (d) views; MGUH 17.376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

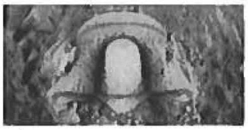

2


1b


3a

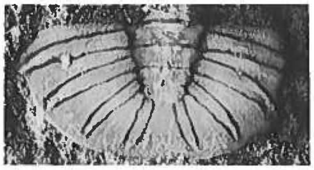

1c

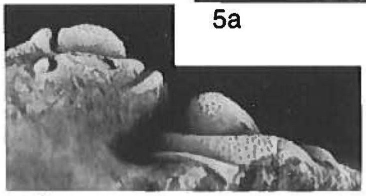

3b

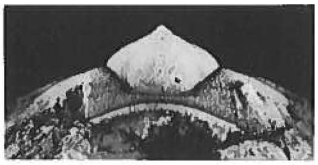

4


5a


5b


6


1d


7c


7a


8b


7b

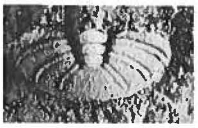

8a


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 ptychoparioid 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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Trilobite and lithofacies relationships in the Holm Dal Formation (late Middle Cambrian), central North Greenland

KENNETH C. HOOD and RICHARD A. ROBISON

Hood, K. C. & Robison, R. A. 1988. Trilobite and lithofacies relationships in the Holm Dal Formation (late Middle Cambrian), central North Greenland. Meddr Grønland, Geosci. 20: 105–112. Copenhagen 1988-12-31.

Multivariate techniques show a strong relationship between trilobite species and lithofacies of the Holm Dal Formation. Presence-absence data on 58 species of trilobites, including 43 polymeroids and 15 agnostoids, were analyzed. Q-mode cluster analysis produced three lithologically homogeneous groups of samples: lime grainstones from Peary Land, lime mudstones from Freuchen Land, and lime mudstones from Peary Land. Nonmetric multidimensional scaling supports the reliability of the Q-mode groups, and stepwise discriminant function analysis indicates that lithology can be discriminated using a four-variable model of *Catillicephala rotunda*, *Hemirhodon* sp., *Marjumia brevifrons*, and *Modocia planata*. R-mode cluster analysis produced four groups of species: grainstone species, Peary Land mudstone species, Freuchen Land mudstone species, and agnostoid species present in all lithofacies. The intersections of Q-mode and R-mode clusters define lithofacies-related faunal associations. These techniques also call attention to samples with unusual faunal compositions and species with unusual distributions.

The distribution of most agnostoids differs from that of most polymeroids, supporting the conclusion that agnostoids were adapted to a different mode of life from that of polymeroids. The distribution of agnostoids was probably controlled by physical and chemical factors that were not dependent on bottom sediment or conditions.

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Quantitative analysis of trilobite data from the Holm Dal Formation (late Middle Cambrian) of central North Greenland (Fig. 1) using multivariate techniques was used to explore patterns of faunal association and environmental control of faunal distribution. Results of these analyses revealed strong lithofacies relationships for some of the Holm Dal fauna and elucidated subtle differences and associations. Presence-absence data on 58 species of trilobites (Robison, this volume, figs 2–6), including 43 species of polymeroids and 15 species of agnostoids, were analyzed. These data are especially suited for evaluation of lithofacies relationships of fauna because many species range through much of the formation and because collections are all from a small geographical area. Differences in faunal associations, therefore, are likely to have resulted from local environmental factors rather than evolutionary changes or geographical isolation.

Trilobites were identified (Robison, this volume) from 34 carbonate samples collected by J. S. Peel of the Geological Survey of Greenland (GGU). Samples were assigned to lithological categories following Dunham (1962) and relate to lithofacies described by Ineson (this volume). The 34 samples include 11 grainstones, 2 packstones, 2 wackestones, and 19 mudstones. The relatively few packstones and wackestones, together with the necessarily arbitrary classification of borderline samples, make it preferable to discuss lithology in terms of the grainstone and mudstone end members. Differences in depositional conditions between grainstone and mudstone end members are more pronounced than if intermediate lithological categories are considered. Affinities of the packstones and wackestones will be discussed subsequently.

To reduce the size of the data matrix and to simplify interpretations, species that are limited to only 1 or 2 collections were eliminated from analyses. Such rare species may be important components of individual collections, but they provide little comparative information and tend to lower similarities. The smaller data matrix contains 41 species, including 30 polymeroids and 11 agnostoids, from 34 collections. Both the complete and the reduced matrices were analyzed with similar results. Therefore, only results based on the smaller matrix are discussed. Binary (presence-absence) data were chosen because samples were neither of uniform size nor of the same ecologic meaning (Kaesler 1966), and the numerical abundance of preserved taxa probably does not represent the original faunal composition (Staff et al. 1986).

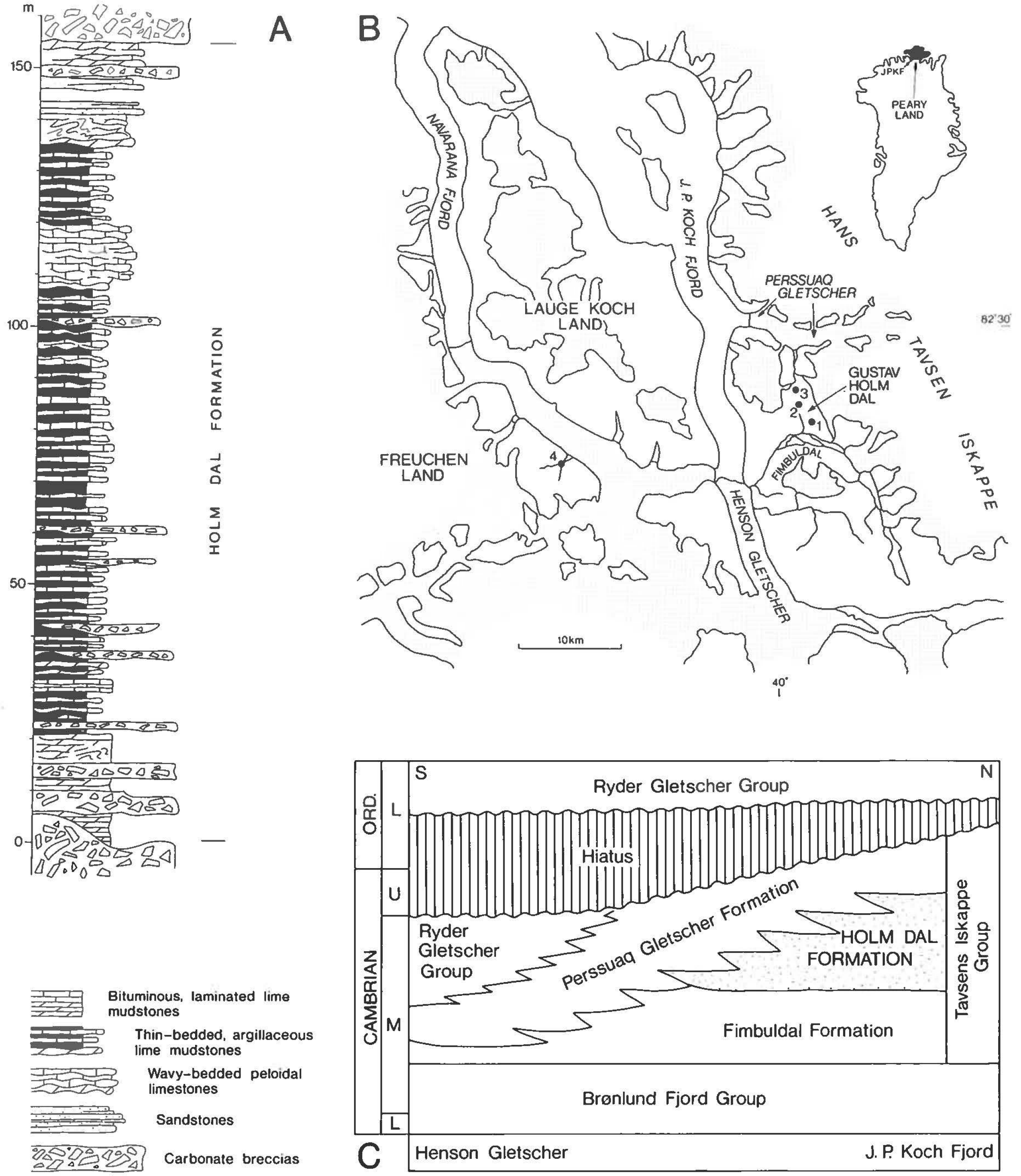

Fig. 1. Geographical and geological relationships of the Holm Dal Formation. A, stratigraphic section through the Holm Dal Formation at its type locality (locality 1 in Fig. 1B; from Ineson, this volume). B, map of the area around Gustav Holm Dal, westernmost Peary Land, central North Greenland showing collection localities within the Holm Dal Formation (1–4). 1, the type section and adjacent area, GGU samples in the sequence 225528–225567; 2, Gustav Holm Dal, GGU samples 225586, 271403, 271404, 271408, 271414, 271417; 3, Gustav Holm Dal, GGU samples 225592–225595; 4, south-east Freuchen Land, GGU samples 315007, 315009, 315011–315013. Inset map of Greenland shows location of Peary Land and J. P. Koch Fjord (JPKF). Full description of trilobites from the respective collections is given by Robison (this volume). C, stratigraphic relationship of the Holm Dal Formation (from Ineson, this volume).

Cluster analyses and nonmetric multidimensional scaling were done using the Numerical Taxonomy System of Multivariate Statistical Programs (NT-SYS; Rohlf et al. 1972), and discriminant function analysis was done using Biomedical Computer Programs (BMDP; Dixon 1983).

Results of analysis

Cluster analysis is a convenient multivariate technique for distinguishing groupings within data (Sokal & Sneath 1963; Sneath & Sokal 1973). Both Q-mode and R-mode cluster analyses were performed. In Q-mode analyses, objects (samples) are related to each other on the basis of their attributes (species). In R-mode analyses, attributes are related to each other on the basis of the objects in which they are found (Hazel 1970). Clustering was performed on a similarity matrix of Jaccard's coefficients (Jaccard 1908) using unweighted pair group arithmetic means (UPGM). Similarity coefficients were used because they generally give more easily interpreted results than distance coefficients (Hazel 1970), and UPGM were used because they produce the smallest amount of distortion (Cheetham & Hazel 1969; Hazel 1970; Rowell et al. 1973). Most of the clusters form at relatively low levels, probably because Jaccard's coef-

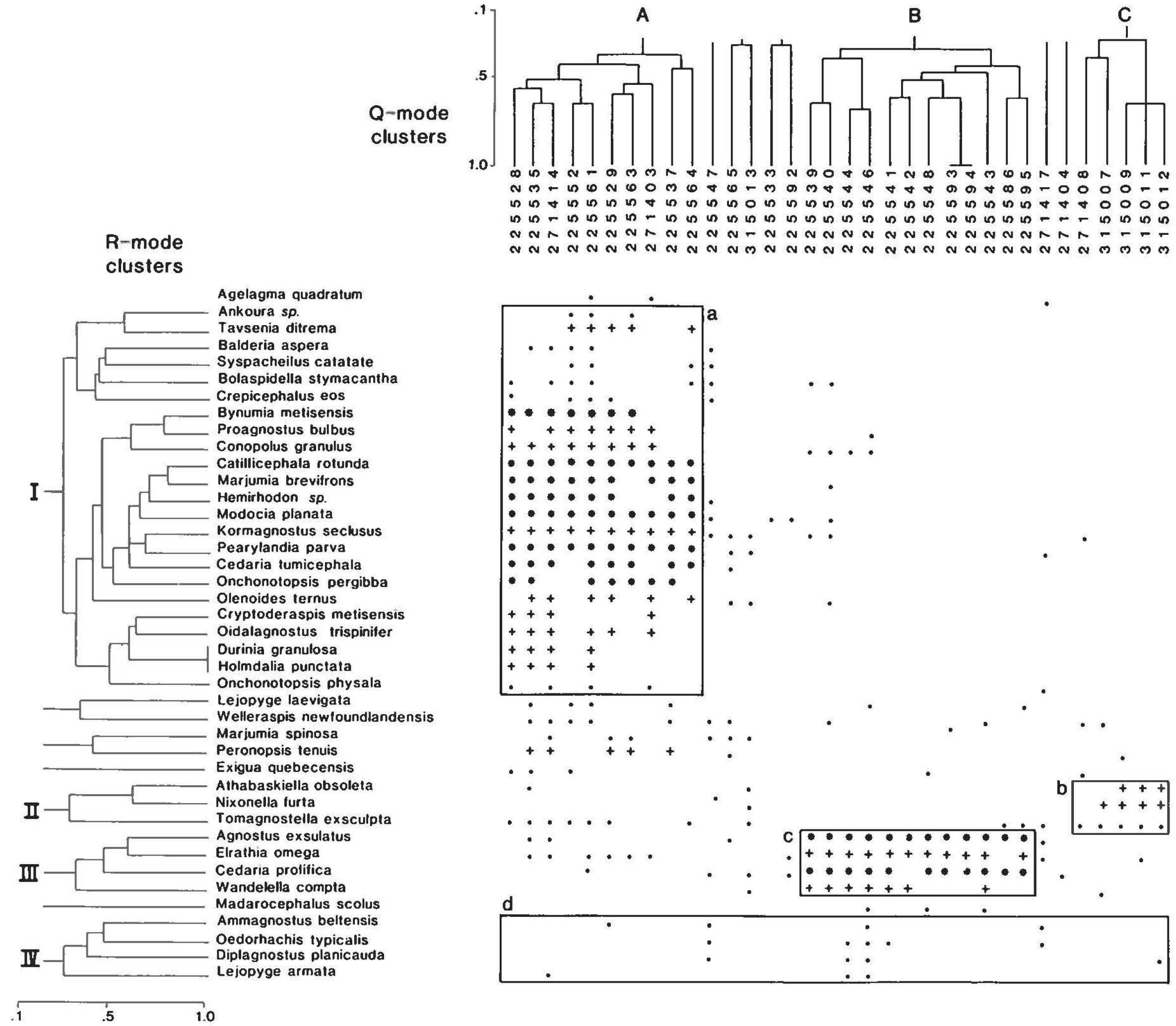

Fig. 2. Data matrix of Holm Dal trilobite species plotted in order formed by Q-mode clustering of collections and R-mode clustering of trilobite species. Meaningful clusters are labeled with roman numerals and capitol letters. The products of fidelity and constancy indices are plotted for each species in each cluster; periods (.) represent values less than or equal to 30, crosses (+) values greater than 30 and less than or equal to 60, and asterisks (*) values greater than 60. The intersection of Q-mode and R-mode clusters define four lithofacies-related faunal associations: grainstone association from Peary Land (a), mudstone association from Freuchen Land (b), mudstone association from Peary Land (c), and agnostoids having weak lithofacies relationships (d). Six-digit numbers are GGU sample numbers.

ficient emphasizes differences within the data (Cheetham & Hazel 1969), and because many species are present in only a small number of collections. Rare species, even with similar environmental adaptations, can have low similarity coefficients due to chance alone. Nevertheless, the clusters seem to represent the effects of real ecologic controls. Clustering was also performed on a similarity matrix of Dice coefficients, which emphasizes similarities (Cheetham & Hazel 1969). The resulting patterns of clustering were identical, differing only in the values of the coefficients.

Q-mode cluster analysis

Q-mode cluster analysis produced three clusters of samples containing similar species (Fig. 2, A-C). Most samples in each cluster are lithologically homogeneous. Cluster A includes 9 grainstones and 1 wackestone from Peary Land. Cluster B includes 11 mudstones and 1 wackestone from Peary Land. Cluster C includes 4 mudstones from Freuchen Land and 1 other mudstone. The species that characterize samples in Q-mode clusters will be discussed under R-mode cluster analysis.

Seven samples, including 3 mudstones, 2 packstones, and 2 grainstones, do not join clusters at meaningful levels and are atypical. For example, Freuchen Land mudstone 315013 contains all three species that characterize other Freuchen Land mudstones, but also contains species that characterize samples in clusters A and B. Consequently, it does not join with any cluster. Grainstone sample 225533 contains only a single specimen of one species, *Modocia planata,* and therefore does not join with the grainstone cluster. Finally, mudstone sample 271404 contains only a single species, *Cedaria prolifica,* and therefore does not join the mudstone cluster.

The reliability of the Q-mode clusters was tested using nonmetric multidimensional scaling (NMDS; Kruskal 1964a, b) because cluster analysis can impose artificial groupings on data. Results of the NMDS (Fig. 3) agree well with the results of the cluster analysis, and samples that form clusters also form reasonably tight groups in two-dimensional NMDS. The first axis represents a contrast between grainstones and mudstones, and the second axis represents a contrast between samples from Freuchen Land and Peary Land.

R-mode cluster analysis

R-mode cluster analysis produced four clusters of species that have similar relationships to lithology (Fig. 2, I-IV). Seven species did not join clusters at levels high enough to be meaningful. In general, cluster I includes species present mostly in grainstones, clusters II and III

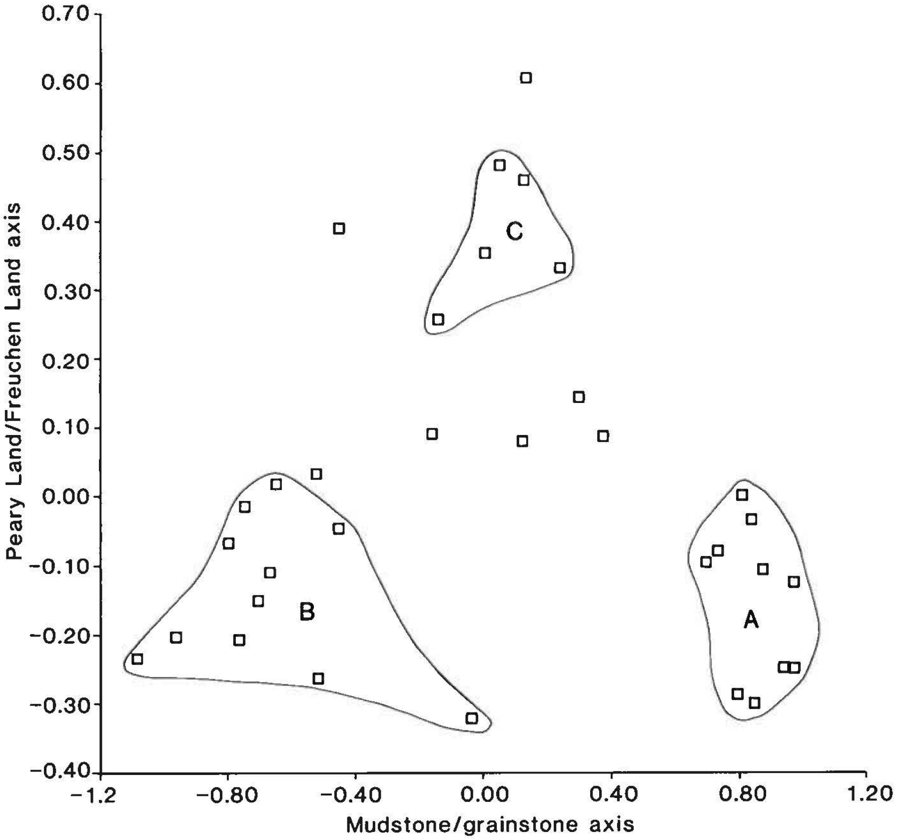

Fig. 3. Nonmetric multidimensional scaling showing the location of samples in two dimensions. The three groups (A-C) correspond to clusters from Q-mode cluster analysis. Group A contains grainstones from Peary Land, group B mudstones from Peary Land, and group C mudstones from Freuchen Land. Samples lying outside groups are the same as those that did not join clusters at meaningful levels.

Table 1. Fidelity (F) and constancy (C) indices for Holm Dal trilobite species in three Q-mode clusters. The number of collections containing a species is listed under N. A hyphen (-) indicates the absence of a species from a cluster.

	Cluster A			Cluster B			Cluster C		
	F	C	N	F	C	N	F	C	N
Agelagma quadratum	7	2	2	–	–	0	–	–	0
Ankoura *sp.*	10	3	3	–	–	0	–	–	0
Tavsenia ditrema	10	5	5	–	–	0	–	–	0
Balderia aspera	8	4	4	–	–	0	–	–	0
Syspacheilus catatate	8	3	3	–	–	0	–	–	0
Bolaspidella stymacantha	6	5	5	3	2	2	–	–	0
Crepicephalus eos	8	4	4	–	–	0	–	–	0
Bynumia metisensis	10	7	7	–	–	0	–	–	0
Proagnostus bulbus	9	7	7	1	1	1	–	–	0
Conopolus granulus	7	8	8	3	3	4	–	–	0
Catillicephala rotunda	10	10	10	–	–	0	–	–	0
Marjumia brevifrons	9	9	9	1	1	1	–	–	0
Hemirhodon *sp.*	9	8	8	–	–	0	–	–	0
Modocia planata	7	10	10	1	1	1	–	–	0
Kormagnostus seclusus	6	10	10	1	2	2	1	2	1
Pearylandia parva	8	10	10	–	–	0	–	–	0
Cedaria tumicephala	9	8	8	–	–	0	–	–	0
Onchonotopsis pergibba	10	7	7	–	–	0	–	–	0
Olenoides ternus	7	6	6	1	1	1	–	–	0
Cryptoderaspis metisensis	10	4	4	–	–	0	–	–	0
Oidalagnostus trispinier	10	6	6	–	–	0	–	–	0
Durinia granulosa	10	4	4	–	–	0	–	–	0
Holmdalia punctata	10	4	4	–	–	0	–	–	0
Onchonotopsis physala	8	3	3	–	–	0	–	–	0
Lejopyge laevigata	6	4	4	4	3	3	–	–	0
Welleraspis newfoundlandensis	5	5	5	2	2	2	2	4	2
Marjumia spinosa	5	3	3	–	–	0	–	–	0
Peronopsis tenuis	7	5	5	–	–	0	1	2	1
Exigua quebecensis	6	3	3	2	1	1	2	2	1
Athabaskiella obsoleta	2	1	1	–	–	0	6	6	3
Nixonella furta	–	–	0	–	–	0	8	8	4
Tomagnostella exsculpta	4	7	7	1	2	2	3	10	5
Agnostus exsulatus	1	2	2	8	10	12	–	–	0
Elrathia omega	3	6	6	6	9	11	1	2	1
Cedaria prolifica	–	–	0	7	9	11	–	–	0
Wandella compta	–	–	0	8	6	7	1	2	1
Madarocephalus scolus	–	–	0	10	3	3	–	–	0
Ammagnostus beltensis	3	1	1	3	1	1	–	–	0
Oedorhachis typicalis	–	–	0	6	3	3	–	–	0
Diplagnostus planicauda	–	–	0	5	2	2	3	2	1
Lejopyge armata	3	1	1	7	2	2	–	–	0

include species present mostly in lime mudstones, and cluster IV includes four agnostoid species having similar distributions. Distributions of the remaining species are not like one another or like those of species forming clusters. More than 70 percent of the collections containing species that join the grainstone and mudstone clusters are grainstones and mudstones respectively. Combining packstones with grainstones and wackestones with mudstones increases the percentage to nearly 80.

Fidelity and constancy indices (cf. Hazel 1970) were computed for each species as measures of how well it characterizes a particular cluster (Table 1). Fidelity is defined by

$$F_{ji} = \frac{N_i}{\Sigma N_i} * 10$$

where N_i is the number of collections in each cluster in which the species is present. It measures the extent to which a species is confined to a cluster. Constancy is defined by

$$C_{ji} = \frac{N_i}{T_i} * 10$$

where T_i is total number of samples in the cluster. It is a measure of the ubiquity of a species in a cluster. Species having both high fidelity and high constancy indices best delimit a cluster.

Cluster I includes 23 species that are more widely distributed in collections from lime grainstones. Species having high fidelity and high constancy indices are *Bynumia metisensis, Catillicephala rotunda, Cedaria tumicephala, Hemirhodon* sp., *Kormagnostus seclusus,* *Marjumia brevifrons, Modocia planata, Onchonotopsis pergibba,* and *Pearylandia parva.* Although some species in the cluster are not restricted to a single lithology, they are more prevalent in grainstones. Cluster I includes several subclusters that appear to be differentiated on the number of collections in which the species occur and not the presence or absence of a species from particular collections.

Clusters II and III include species that are more widely distributed in collections from lime mudstones. Cluster II contains three species, *Athabaskiella obsoleta, Nixonella furta,* and *Tomagnostella exsculpta,* that characterize mudstones from the Freuchen Land section. *T. exsculpta* is present in all lithologies, but groups with species from Freuchen Land because it is in all five of the collections. Cluster III contains four species, *Agnostus exsulatus, Cedaria prolifica, Elrathia omega,* and *Wandelella compta,* that characterize mudstones from Peary Land sections. *E. omega* is present in all lithologies and was probably eurytopic, but is relatively more widespread in mudstones. Only *N. furta* is restricted to collections from Freuchen Land. Several other species are present in mudstone collections from both Freuchen Land and Peary Land. This suggests that faunal composition varies because of subtle environmental differences at the time of deposition rather than geographic isolation. The mudstone species seem to indicate a stronger relationship to environment than to lithology, because the mudstone samples from Peary Land and Freuchen Land are not noticeably different.

Cluster IV contains four agnostoid species whose distribution is independent of lithology. As a group, these species are present in grainstones, packstones, wackestones, and mudstones, although each occurs in only a small number of collections. They group together because they are present in several of the same collections.

Some information can also be gleaned about species that do not join clusters. Five species, *Exigua quebecensis, Lejopyge laevigata, Marjumia spinosa, Peronopsis tenuis,* and *Welleraspis newfoundlandensis,* are somewhat more widespread in grainstones but do not join the grainstone cluster at meaningful levels. These species may have been relatively eurytopic, and their distributions in collections are neither similar to one another nor to the distributions of grainstone species. Two of the five species are agnostoids.

The distribution of *Agelagma quadratum* is unlike that of any other species and it joins no cluster at a meaningful level, perhaps owing to its presence in only a few collections. *A. quadratum,* however, is the only polymeroid species in the Holm Dal fauna having intercontinental distribution. Its morphology, small size, and geographic distribution collectively are in accord with an inferred pelagic mode of life (Robison, this volume).

Madarocephalus scolus also does not join a cluster at a meaningful level. It is present in only three collections, all part of the Peary Land mudstone cluster. *M. scolus* is, on average, the smallest trilobite in the Holm Dal Formation, and could have been more readily transported than larger trilobites. It is possibly the only spe-

GGU sample	Incorrect classification
grainstones	
225528	
225529	
225533	mudstone
225537	
225547	
225552	
225561	
225563	
225564	
271403	
packstones	
225565	mudstone
271417	mudstone
wackestones	
225548	mudstone
271414	grainstone
mudstones	
225539	
225540	
225541	
225542	
225543	
225544	
225546	
225586	
225592	grainstone
225593	
225594	
225595	
271404	
271408	
315007	
315009	
315011	
315012	
315013	

Table 2. Classification of samples for discriminant function analysis. Samples are in lithological categories, and classifications are listed for samples that were misclassified. All samples were classified as either grainstones or mudstones. Six-digit numbers are GGU sample numbers.

cies found in the mudstone facies that was transported in from other environments.

Discriminant function analysis

Stepwise discriminant function analysis (Morrison 1976) was performed to determine independently how well samples could be separated into lithological categories and to determine which linear combination of species provides the best separation. Lithology was selected as the grouping variable because it is readily predetermined and because the cluster analyses suggested that species presence varied with lithology. Samples can be discriminated into grainstone and mudstone end members with a four-variable model of *Catillicephala rotunda, Hemirhodon* sp., *Marjumia brevifrons,* and *Modocia planata.* Jack-knife classification of grainstones and mudstones was 93 percent correct (Table 2). Jack-knife estimators are conservative and reliable when compared to standard estimators (Neff & Marcus 1980).

The classifications mostly agree with the results of the cluster analysis, suggesting that the results are reliable. The two grainstone and mudstone samples that were misclassified (225533, 225592) also did not join clusters at meaningful levels. With respect to the discriminant model, one wackestone (271414) was classified with grainstones and one (225548) with mudstones. Both packstones (271417, 225565) were classified with mudstones. A histogram of the canonical variable shows the separation of grainstones and mudstones (Fig. 4). Discriminant function analysis using four lithological categories produced less satisfactory results, probably because of the small number and high faunal variability of wackestones and packstones.

Discussion

Study of trilobite data from the Holm Dal Formation by multivariate techniques indicates a relationship between the presence of species and lithology. Q-techniques generally group samples into lithologically homogeneous categories on the basis of contained species, suggesting that the degree of lithofacies relationship for many species is high. These techniques also bring to attention samples that are unusual either because they contain a mixture of species that characterize different lithologies or because they lack several species that characterize a single lithology. Ineson (this volume) includes most of the Holm Dal mudstones in a single lithofacies (argillaceous lime mudstone). Grainstones, however, are included in two lithofacies (wavy-bedded peloidal limestone and grainstone laminae within argillaceous lime mudstone). Therefore, the lithological determinations used in this study do not correspond exactly with the lithofacies of Ineson, but the groups of samples produced by Q-techniques are similar. The Q-techniques allow further subdivision of mudstone samples into two groups.

R-techniques allow species to be grouped into those present mostly in grainstones, those mostly in Peary Land mudstones, those mostly in Freuchen Land mudstones, and those distributed through all three categories. In addition, the results allow comparison of the distributions of polymeroids and agnostoids. Of the species present in a large number of collections, only two, *Tomagnostella exsculpta* (agnostoid) and *Elrathia omega* (polymeroid), are evenly distributed among all lithologies. Nine of the less common species are relatively independent of lithology; of these, six are agnostoids. In

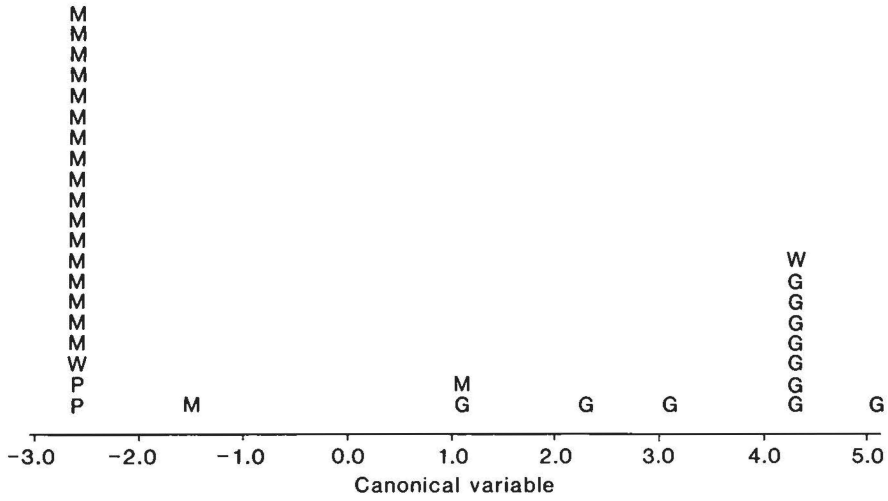

Fig. 4. Histogram showing the separation of grainstones (G) and mudstones (M) on the canonical variable and the affinities of packstones (P) and wackestones (W) with respect to the discriminant model. Mudstone and grainstone samples that plot together in the centre of the axis were misclassified by the model.

all, 7 of 11 agnostoids (64 percent) are relatively independent of lithology, whereas only 4 of 29 polymeroids (14 percent) are. This difference is consistent with the conclusion that agnostoids were mostly pelagic and polymeroids were mostly benthic (Robison 1972). In contrast, *Agnostus exsulatus, Kormagnostus seclusus,* and *Oidalagnostus trispinifer* show strong lithofacies relationships. *A. exsulatus* is found mostly in mudstones, possibly because of adaptation to more oceanic environments. *K. seclusus* and *O. trispinifer,* however, are found mostly in grainstones, possibly because of adaptation to more neritic environments. A similar pattern of distribution of agnostoids was reported by Jago (1973). The distribution of agnostoids was probably controlled in part by changes in salinity, nutrients, or other physical and chemical factors that were not causally related to changes in lithology.

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The arthropod trail *Multipodichnus* from the upper Middle Cambrian (Holm Dal Formation) of central North Greenland.

JAN BERGSTRÖM and J. R. INESON

Bergström, J. & Ineson, J. R. The arthropod trail *Multipodichnus* from the upper Middle Cambrian (Holm Dal Formation) of central North Greenland. Meddr Grønland, Geosci. 20: 113–117. Copenhagen 1988-12-31.

A *Cruziana*-like trace fossil is described from the uppermost beds of the Holm Dal Formation in its type locality in western Peary Land. Lower stratigraphic levels within the same formation yield rich faunas of late Middle Cambrian age. The trace has its closest known counterparts in freshwater deposits from the Permian and Triassic.

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The trace fossil described here was collected from the upper levels of the Holm Dal Formation in its type section in western Peary Land, central North Greenland (Fig. 1). The upper Middle Cambrian Holm Dal Formation is a constituent formation of the Tavsens Iskappe Group and forms part of the carbonate-dominated marine shelf sequence of the Early Palaeozoic Franklinian basin which extends from Arctic Canada eastward across North Greenland. Discussion of the regional setting and the stratigraphy of the Holm Dal Formation is given by Ineson (this volume) while papers by Robison, Hood & Robison, Zell & Rowell and Peel (all this volume) describe the fauna.

The Holm Dal Formation is 155 m thick in its type section and is dominated by subtidal argillaceous lime mudstones of deep, outer-shelf aspect. It forms the lower part of a large-scale regressive cycle and is succeeded by platform-edge, shallow water carbonate and siliciclastic sediments of the Perssuaq Gletscher Formation (Fig. 1). This upward-shallowing trend is reflected in the Holm Dal Formation itself by the appearance of winnowed peloidal grainstones and packstones, and flaggy siliciclastic sandstones in the upper levels of the formation.

The trace fossils described below occur within the interval of pale yellow-brown weathering sandstones near the top of the formation (Fig. 1). The sandstones are very fine-grained to fine-grained, moderately to well sorted and typically bioturbated, although locally displaying current ripple cross-lamination. Further discussion of this facies is given by Ineson (this volume). The environment of deposition is broadly interpreted as the proximal zone of the outer shelf.

The precise age of the trace fossils is not established. Lower levels within the Holm Dal Formation have yielded a diverse fauna within which trilobites are conspicuous (Robison, this volume). Robison notes that the dominant polymeroids belong to species and genera characteristic of the lower and middle *Cedaria* Zone of North American usage. However, accompanying agnostoid species are characteristic of the *Lejopyge laevigata* Interval-zone indicating a late Middle Cambrian age in terms of the Swedish standard for north-western Europe. A similar age is assumed for the specimens of *Multipodichnus*.

Multipodichnus Walter, 1984

Multipodichnus holmi n. ichnosp.

Figs 2–6

Name. – In reference to the type locality in Gustav Holm Dal.

Material. – One slab with 8 clearly distinguishable trackways collected by J. R. Ineson in 1979 from the Holm Dal Formation in Gustav Holm Dal, western Peary Land, central North Greenland. The slab is preserved in the Geological Museum, Copenhagen; figured specimens are numbered MGUH 18.668–18.670 from GGU sample 218655.

Definition. – Species of *Multipodichnus* in which the main bend of the individual track is more distally placed

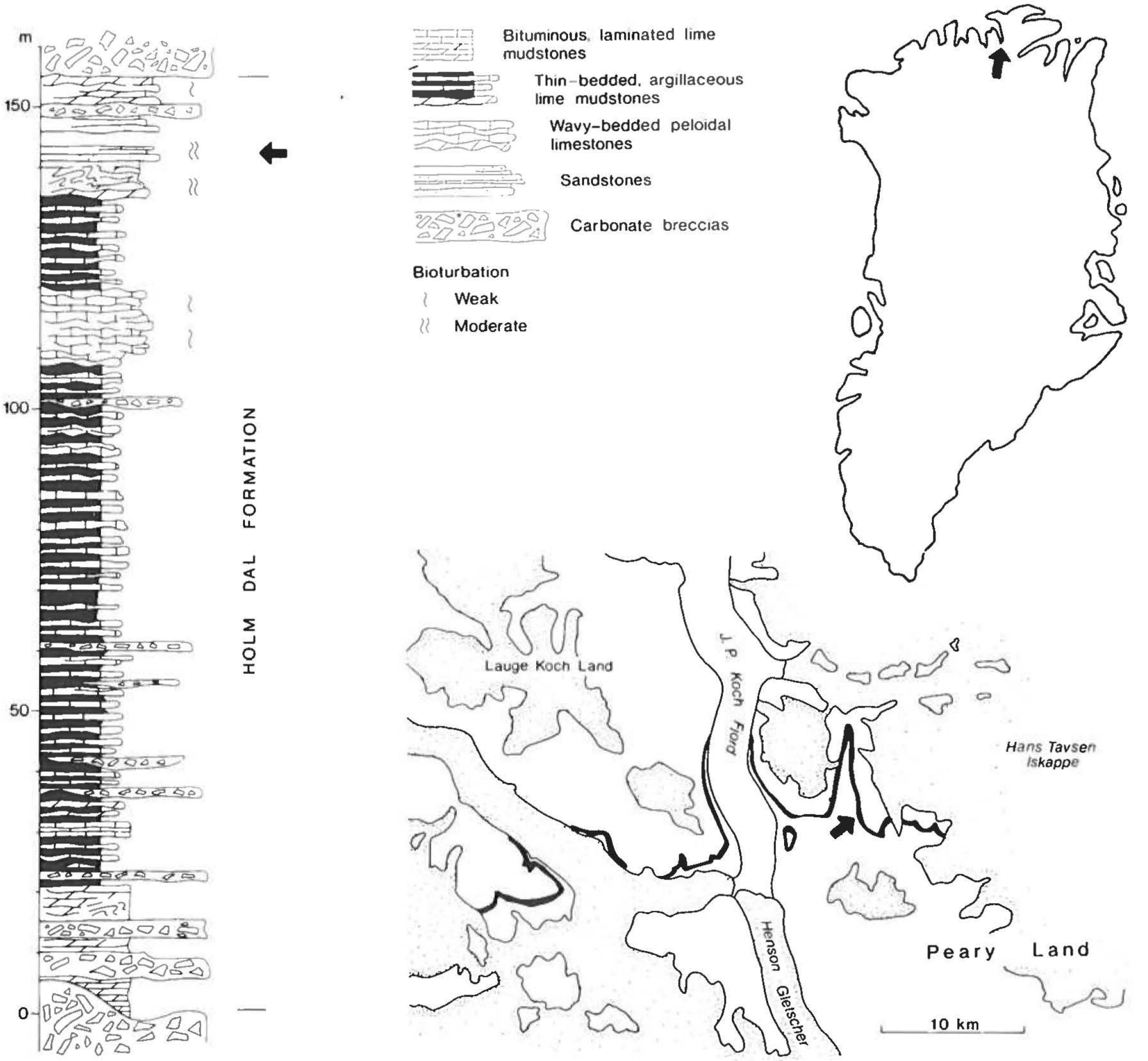

Fig. 1. Location and stratigraphy of the Holm Dal Formation in central North Greenland. Arrows mark the horizon yielding *Multipodichnus holmi* n. sp. in the type section of the formation, and the location of the type section.

than in the type species *M. reptatus;* well preserved specimens show traces of short setae or spines.

Description. – The upper surface of the thin slab of very fine-grained sandstone has a number of 3–16 mm wide and slightly curving trails. These are preserved in epirelief. Each trail consists of paired imprints of a curved limb outline, with the convexity directed posteriorly. The sediment is pushed up at the posterior extremity, while an evenly sloping concavity is formed in front. In a few cases this concavity exhibits setal imprints, numbering up to at least five in one track. The setal scratches from both sides converge backwards, the angle of the V being about 40–45 degrees. The limbs therefore were swung around an axis which differed some 20 degrees from the transverse line.

One point of variation is the depth of impression. In one large trail the limbs were so deeply impressed that their outline is shown to the midline of the trail (Figs 4, 5). In most trails, however, there are only tracks showing the more distal parts of the limbs (Figs 2, 3, 6). Individual trails show a straighter outline of the limb tracks, probably because the limbs were held at a greater angle to the sediment surface when the tracks were made. There is a gradation between the extremes showing that they belong together.

In a few cases there is some indication that the track pairs were arranged in V-shaped series consisting possibly of some 6–7 pairs (Fig. 6).

Discussion. – This trace fossil is reminiscent of traces referred to *Cruziana* and *Diplichnites*. However, it can

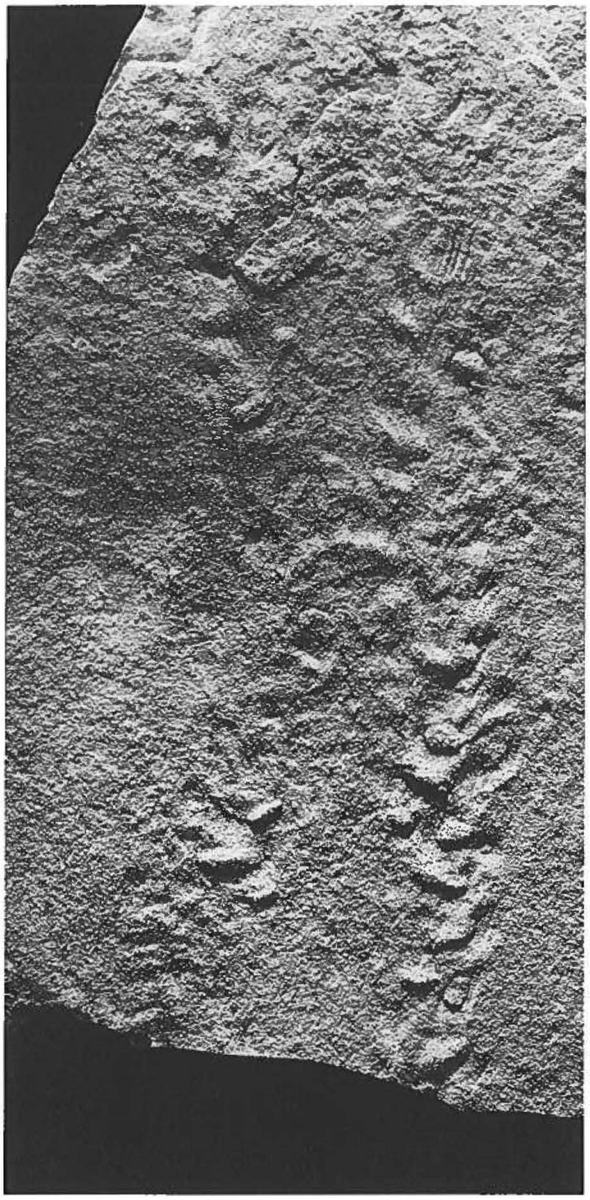

Fig. 2. *Multipodichnus holmi* n. sp., trackway with imprints of setae in the individual tracks. Holotype, MGUH 18.668 from GGU 218655, Holm Dal Formation, Gustav Holm Dal, Peary Land, central North Greenland, X 3.

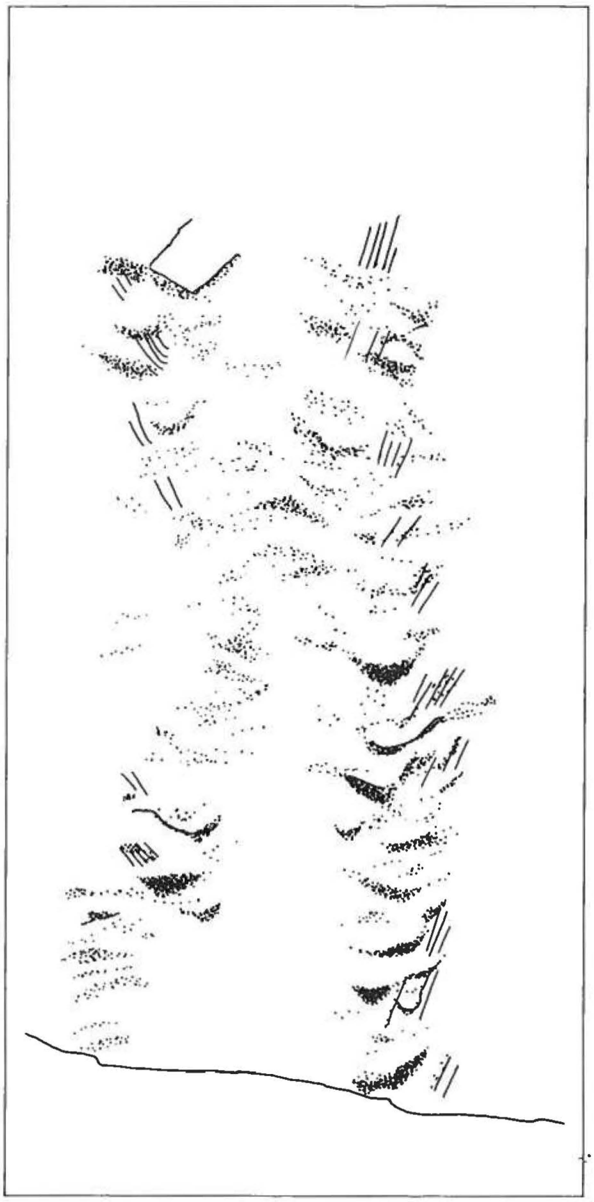

Fig. 3. *Multipodichnus holmi* n. sp., sketch of the holotype (Fig. 2) showing trackway with imprints of setae in the individual tracks.

not be referred to these genera because the individual tracks were formed by a foliaceous kind of limb provided with short terminal setae. In *Cruziana* and *Diplichnites* the tracks were instead formed by a pediform endopod and/or by a rake-shaped exopod. The most similar track described in the literature is *Multipodichnus reptatus*, described by Walter (1983) from the Rotliegendes (Lower Permian) of the German Democratic Republic and the trace described herein is at least provisionally referred to the same genus. However, there is a great time discrepancy between the two occurrences, and the Permian trace was made in a non-marine environment. It is not suggested that *M. reptatus* and *M. holmi* were produced by phylogenetically related animals.

Another trace that is similar to *Multipodichnus holmi* was described as *Cruziana* sp. B by Bromley & Asgaard (1979: fig. 19) from Triassic freshwater strata at Carlsberg Fjord, East Greenland. Like *M. holmi*, this trace consists of serially repeated lobes which show an over-

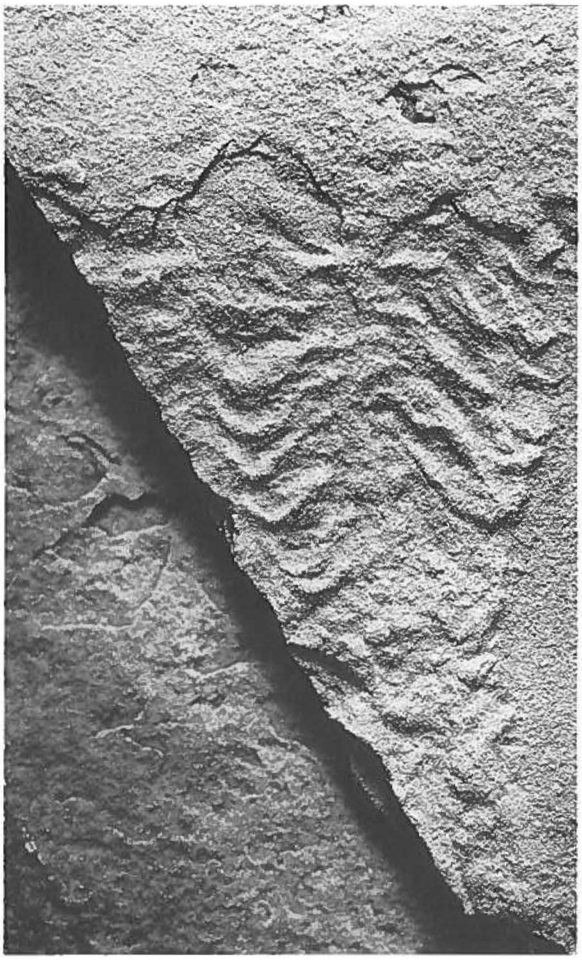

Fig. 4. *Multipodichnus holmi* n. sp., trackway with outlines of track-producing foliaceous appendages. MGUH 18.669 from GGU sample 218655, Holm Dal Formation, Gustav Holm Dal, Peary Land, central North Greenland, X 3.

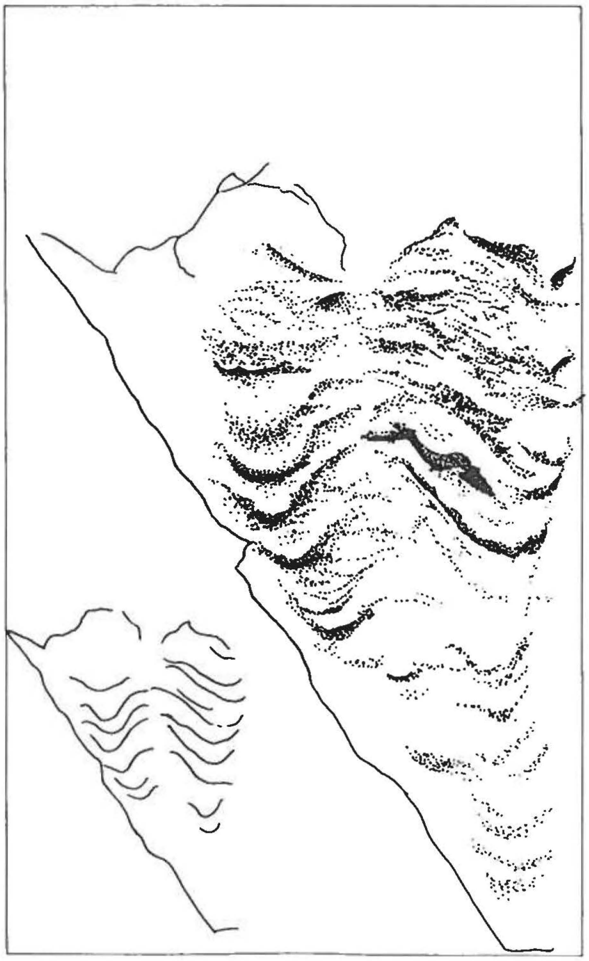

Fig. 5. *Multipodichnus holmi* n. sp., sketch of the specimen illustrated in Fig. 4 showing trackway with outlines of track-producing foliaceous appendages; small figure showing the crests of the individual tracks, X 2.

lapping, imbricated relationship in places, and commonly have an arcuate form. Weak striae are seen locally. The trails vary considerably in shape and Bromley & Asgaard believe that they are probably endogene variants of the associated *Cruziana problematica* or *Diplichnites triassicus*. A similar interpretation may apply for *M. holmi*, although there are no preserved trail types with which it can be associated.

The limb in the animal responsible for making the trace assigned to *M. holmi* was moved backwards-inwards in the track-making stroke. This direction of movement is commonly seen in *Cruziana* and *Rusophycus*, trace fossil genera generally held to have been produced by trilobitomorph arthropods. In phyllopods with foliaceous limbs, on the other hand, the limbs presumably would have moved straight backwards. In principle, the limb of notostracan phyllopods can produce tracks of the general type found in *M. holmi* (Trusheim 1931; Bromley & Asgaard 1972). The Middle Cambrian *Branchiocaris* from the Burgess Shale has foliaceous limbs with an outline that would seem to fit the trace-maker (Bergström, unpublished observation), but again the basal hinge of the limb appears to be strictly transverse, which makes the backwards-inwards movement impossible.

There is a variety of marine Cambrian arthropods other than trilobitomorphs known for instance from the Burgess Shale, but as a rule the limbs are too poorly known to allow a serious discussion of those arthropods as possible trace-makers. The conclusion regarding the systematic position of the trace-maker is therefore that it was an arthropod of unknown affinities.

Acknowledgements

Dr. Richard G. Bromley gave valuable scientific and linguistic advice which is gratefully acknowledged.

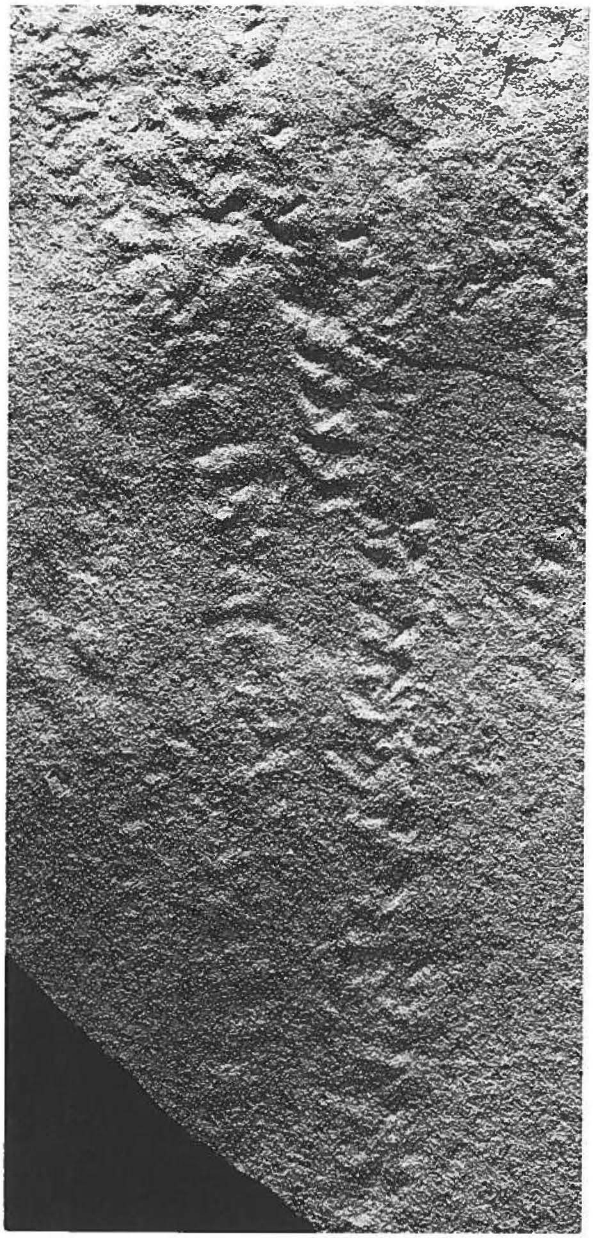

Fig. 6. *Multipodichnus holmi* n. sp., trackway with indication of V-shaped pattern. MGUH 18.670 from GGU sample 218655, Holm Dal Formation, Gustav Holm Dal, Peary Land, central North Greenland, X 3.

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

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Zell, M. G. & Rowell, A. J. 1988. Brachiopods of the Holm Dal Formation (late Middle Cambrian), central North Greenland. Meddr Grønland, Geosci. 20: 119–144. Copenhagen 1988-12-31.

Brachiopods from the Holm Dal Formation are all inarticulates and some 70 percent belong to genera that had an intercontinental Cambrian distribution. The majority of the genera have relatively long stratigraphic ranges; because they are only moderately eurytopic, their chronostratigraphic resolution is modest. The species, however, are more strongly endemic than the genera and consist largely of forms that are known only from North Greenland or are referred to taxa whose distribution is limited to platforms around Cambrian Laurentia; only one species is known from another continent. The fauna consists of 14 species referred to 11 genera of which none of the latter are new. Six of the species are retained in open nomenclature because of limited material or inadequate information. Three of the species are new: *Canthylotreta grada, Dactylotreta patriella,* and *Anabolotreta groenlandica.*

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The Holm Dal Formation of central North Greenland is defined in an accompanying paper by Ineson (this volume; see also Fig. 1) who provides stratigraphic data and locality information for the brachiopods that are discussed here. Ineson also describes the depositional setting of the unit, which accumulated on an open shelf and associated slope during late Middle Cambrian time.

The Holm Dal Formation is a very fossiliferous segment of the stratigraphic column, although the upper approximately 30 m of the formation have only yielded trace fossils (Bergström & Ineson this volume). Brachiopods, all of which are inarticulates, form only a minor part of its fauna. The 14 recognised species are distributed among three orders (Table 1). Molluscs are a small but significant component of the benthos, and these are described by Peel (this volume). The preserved fauna is dominated by trilobites whose 58 species are documented by Robison (this volume). They include the cosmopolitan agnostoids and the more endemic polymeroids. The agnostoids demonstrate that the fossiliferous part of the Holm Dal Formation lies within the upper *Lejopyge laevigata* Interval zone and although the polymeroids include taxa that are found in three North American biozones, they are most similar to the faunas of the lower and middle *Cedaria* Zone (Robison this volume).

The brachiopods show stratigraphic and geographic distribution patterns that are intermediate between those of the agnostoids and those of polymeroid trilobites. At the generic level, the brachiopods are much more cosmopolitan than polymeroids because 8 of 11 brachiopod genera are not restricted to shelves around Cambrian Laurentia (in the sense of Bambach et al. (1980) to include most of North America and Greenland, together with part of Scotland). Nevertheless, the genera have limited biostratigraphic utility for intercontinental correlation: seemingly they were only moderately eurytopic and other aspects of larval distribution also may have slowed their dispersion across world oceans. Indeed, three genera, *Curticia* Walcott 1905, *Canthylotreta* Rowell 1966, and *Rhondellina* Rowell 1986, are known only from North America and Greenland. At the species level, the endemism of inarticulate brachiopods is broadly comparable with that of polymeroid trilobites. Only one species, *Linnarssonia tumida* Henderson & MacKinnon 1981, is known to have an intercontinental distribution. The remaining species are either restricted to North Greenland or have been recorded only from shelf and slope deposits around Laurentia.

Inarticulate brachiopods are difficult to study unless they can be etched free from their carbonate matrix by dilute formic or acetic acid. The technique is capable of yielding superb examples, unfortunately the majority of the specimens recovered from the insoluble residues of the North Greenland collections consist of only fragments of the more robust part of the valves. A few of the fragments are obviously worn and the valves were probably broken before they were entombed. Most valves, however, are not severely abraded and may

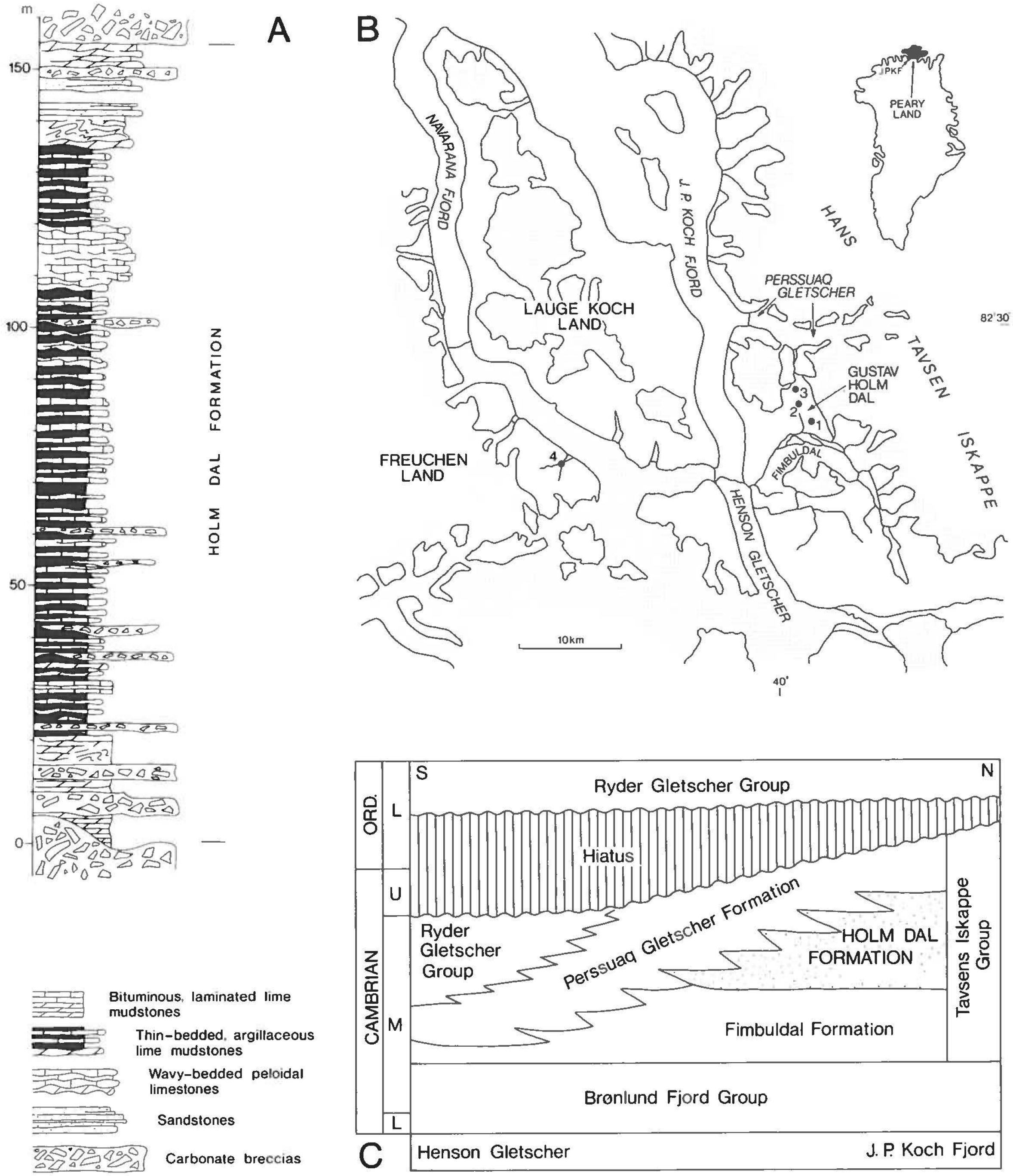


Fig. 1. Derivation of inarticulate brachiopods from the Holm Dal Formation, central North Greenland. A, Stratigraphic section through the Holm Dal Formation at its type locality (locality 1 in Fig. 1B; from Ineson, this volume). B, map of the area around Gustav Holm Dal, westernmost Peary Land, central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

Table 1. The brachiopod fauna of the Holm Dal Formation.

Class Inarticulata
Order Acrotretida
  Superfamily Acrotretacea
  Family Acrothelidae
    Orbithele sp.
  Family Acrotretidae
  Subfamily Acrotretinae
    Canthylotreta marjumensis (Walcott)
    Canthylotreta grada n. sp.
    Prototreta sp.
    Dactylotreta patriella n. sp.
  Subfamily Linnarssoniinae
    Linnarssonia tumida Henderson & MacKinnon
    Anabolotreta groenlandica n. sp.
    Picnotreta sp.
  Subfamily unassigned
    Rhondellina dorei Rowell
  Family Curticidae
    Curticia minuta Bell
Order Paterinida
  Superfamily Paterinacea
  Family Paterinidae
    Micromitra cf. *M. modesta* (Lochman)
Order Lingulida
  Superfamily Lingulacea
  Family Obolidae
    Lingulella sp. 1
    Lingulella sp. 2
    Lingulella sp. 3

have been cracked after burial by diagentic compaction.

The new distributional data from North Greenland are interesting because several genera occur in associations that are presently unknown elsewhere in the world. Fig. 2 shows diagrammatically the previously known stratigraphic ranges of genera that occur in the Holm Dal Formation. The brachiopod fauna is consistent with the formation being of late Middle Cambrian age. Indeed, this age is the most parsimonious interpretation of the data (Fig. 2); with it, the stratigraphic ranges of two genera are lowered and those of two others are raised.

Systematic descriptions

Terminology. – The terminology used for morphological features is largely that employed in the Treatise on Invertebrate Paleontology Part H (Moore 1965). We also use some terms, particularly for features of the Acrotretacea, that were defined by Krause & Rowell (1975).

Stratigraphic distribution. – The distribution of brachiopods and accompanying trilobites and molluscs is shown in Figs 3–7.

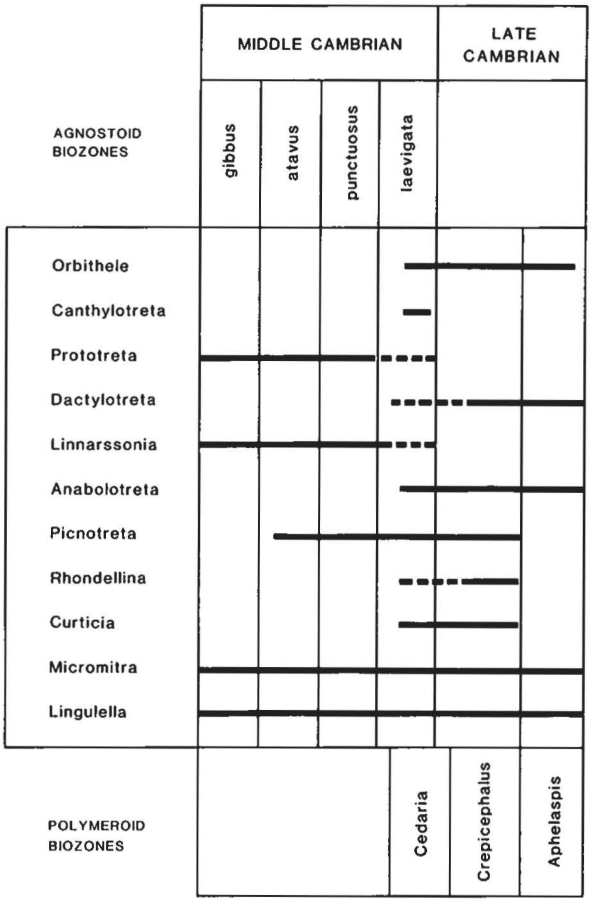


Fig. 2. Diagrammatic representation of the stratigraphic distribution of inarticulate brachiopod genera that occur in the Holm Dal Formation. Ranges are plotted on a sequence of biostratigraphic zones that are interpreted as informal chronozones for the purpose of the figure. Extension of previously known ranges shown by broken lines.

It should be noted that with the exception of the trace fossils described by Bergström & Ineson (this volume), no fossils were collected from the upper 30 m of the Holm Dal Formation in Peary Land (localities 1–3 in Fig. 1B; Figs 3–6). Fossiliferous collections from locality 4 in Freuchen Land are derived from the lowest 50 m of the formation (Fig. 7).

Depositories. – Collection sample numbers for all Geological Survey of Greenland (Grønlands Geologiske Undersøgelse) material used in this study are prefixed by GGU. Figured and type specimens bear additionally a specimen number prefixed by MGUH; they are housed in the Geologisk Museum (formerly the Mineralogisk Museum), Copenhagen. The remaining non-illustrated specimens are deposited in the collections of the Geological Survey of Greenland, Copenhagen.

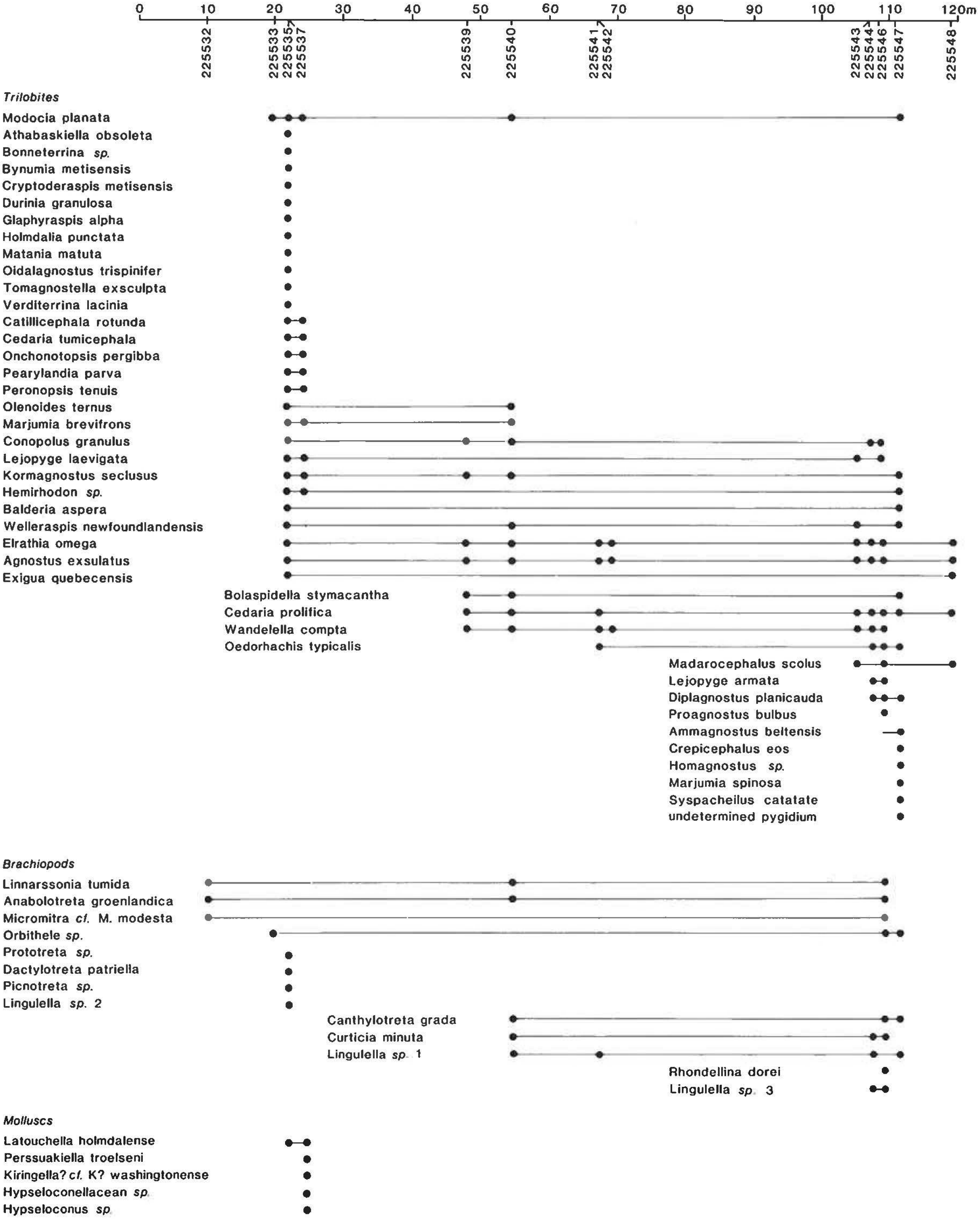


Fig. 3. Stratigraphic distribution of trilobites, brachiopods and molluscs from the type section of the Holm Dal Formation (Fig. 1A, locality 1 in Fig. 1B). Six-digit numbers are GGU collection numbers. The formation is almost 155 m thick in its type section; scale indicates height above the base of the formation.

Fig. 4. 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 its type section (see Fig. 3). Collections are not in stratigraphic sequence.

	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.*			●						

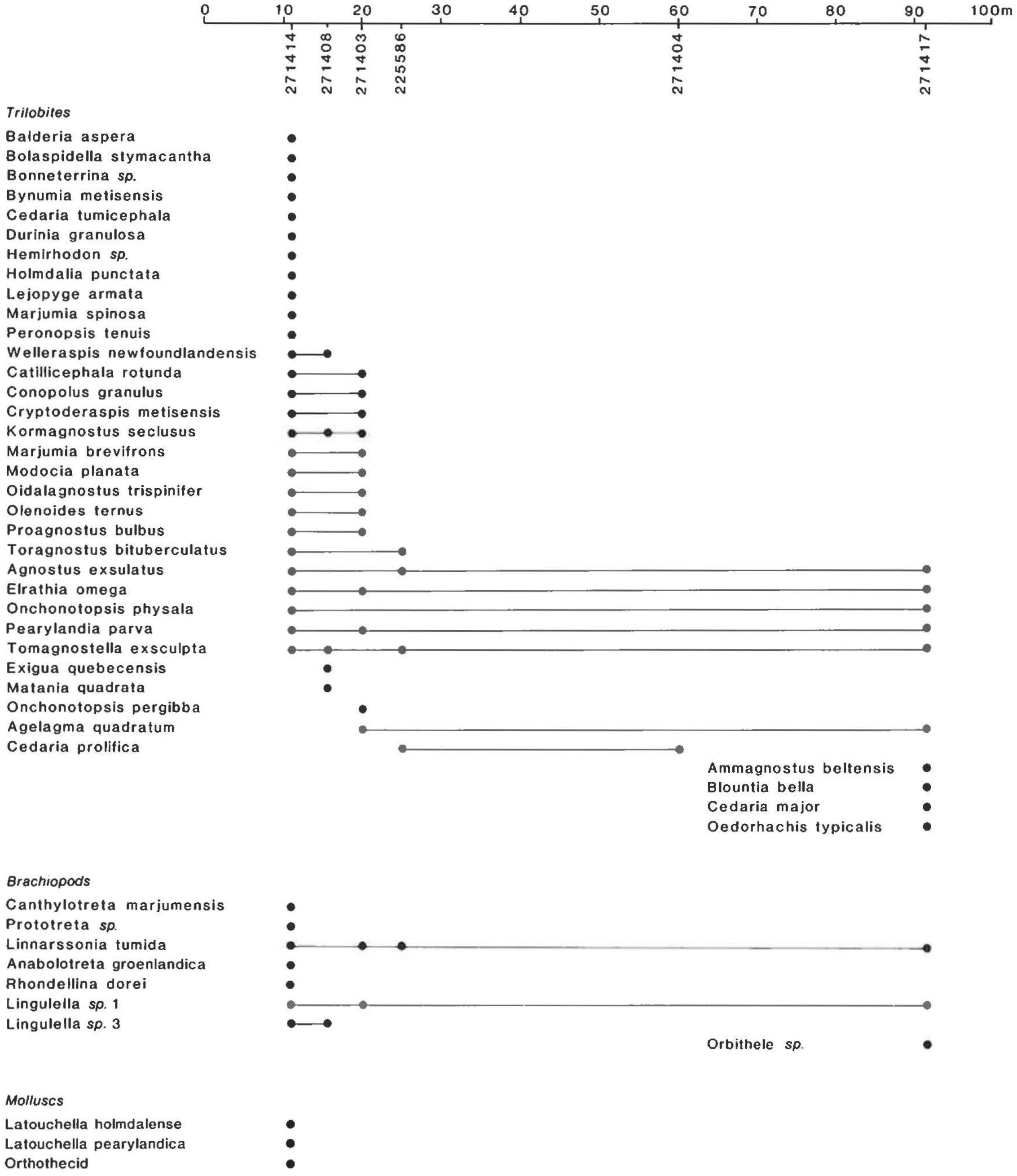


Fig. 5. Stratigraphic distribution of trilobites, brachiopods and molluscs in GGU collections (six-digit numbers) from locality 2 (Fig. 1B) of the Holm Dal Formation. Scale indicates height above the base of the formation.

Order Acrotretida
Superfamily Acrotretacea
Family Acrothelidae

Genus Orbithele Sdzuy 1955

Type species. – *Discina contraria* Barrande 1868, p. 104, fig. 72; by original designation.

Remarks. – *Orbithele* and *Acrothele* Linnarsson 1876 are two phenetically similar genera that are judged to be closely related following cladistic analysis. *Acrothele* is a common Middle Cambrian genus; *Orbithele*, whose known stratigraphic range slightly overlaps that of *Acrothele*, is more common in the Upper Cambrian, but occurs also in the Lower Ordovician of Czechoslovakia (Mergl 1981). The principal morphological difference between the two is that *Orbithele* possesses a ventral internal pedicle tube. Seemingly, spines developed differently on the larval valves (Rowell 1980), but this merits further investigation. In the few species of *Orbithele* that have been examined at the appropriate magnification, the dorsal larval valve bears four relatively long spines that are arranged symmetrically. In contrast, the type species of *Acrothele*, *A. coriacea* Linnarsson 1876, and the common Great Basin species, *A. subsidua* (White 1874), have at least the anterior pair of projections as low nodes (Rowell 1980).

Trilobites	225592	225593	225594	225595
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. 6. Trilobites and brachiopods in GGU collections (six-digit numbers) 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, GGU 225594 and 225595 are from near the top of this fossiliferous interval.

Orbithele sp.

Fig. 8.1–3

Material. – Five ventral and two dorsal valve fragments, together with one articulated juvenile shell from GGU samples 225533, 225546, 225547 and 271417. Unidentifiable acrothelids were also found in GGU sample 225561.

Remarks. – Because the available material is fragmentary and poorly preserved, or is juvenile, these specimens are left in open nomenclature. Three of the ventral valves retain indications of the pedicle tube, but it is intact in only one of them. The larval shells possess the coarse pitting characteristic of all known acrothelids (Figs 8.1d-f; see also Rowell 1980). The distribution of spines in these larval valves is consistent with the material being *Orbithele*, but the spines are all broken near their tip.

Occurrence. – Rare in the basal part of the Holm Dal Formation, and near the top of the fossiliferous sequence at localities 1 and 2 (Figs 1, 3, 5).

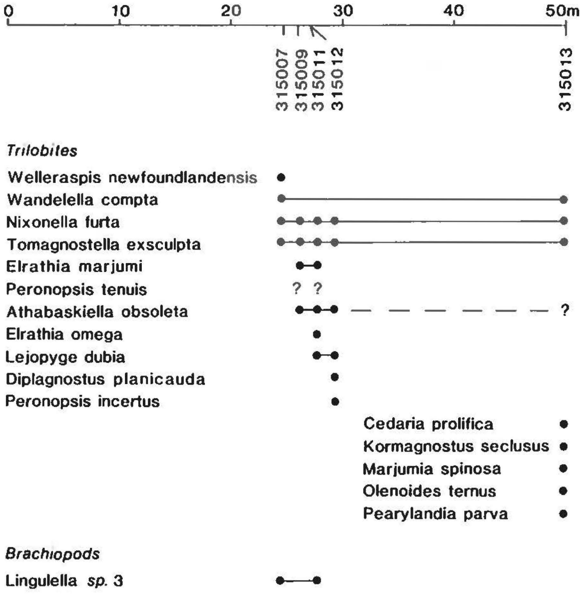


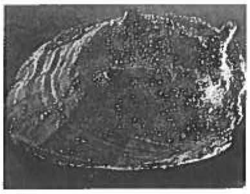
Fig. 7. Stratigraphic distribution of trilobites and brachiopods from locality 4 (Fig. 1B) of the Holm Dal Formation in GGU collections (six-digit numbers) from south-east Freuchen Land. Scale indicates height above the base of the formation.

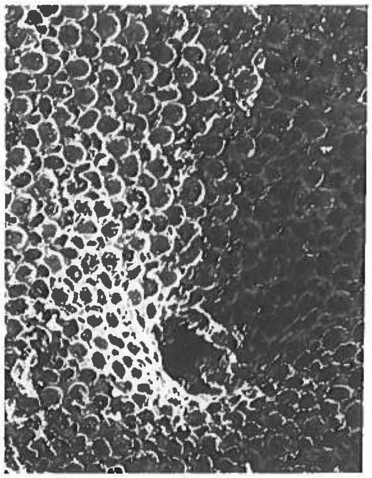

1a


2a


1b


2b

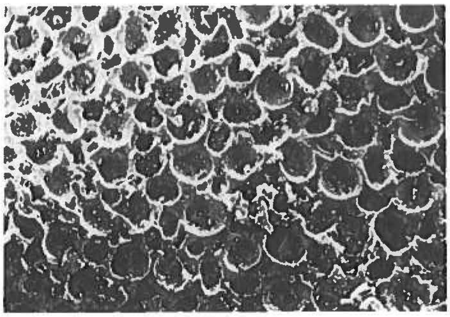

1c

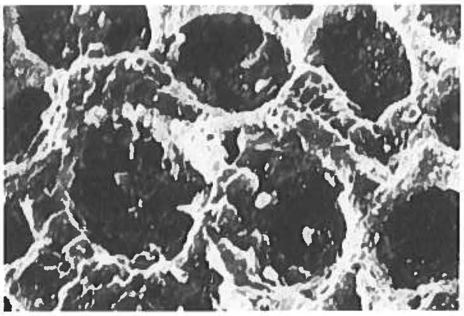

1d

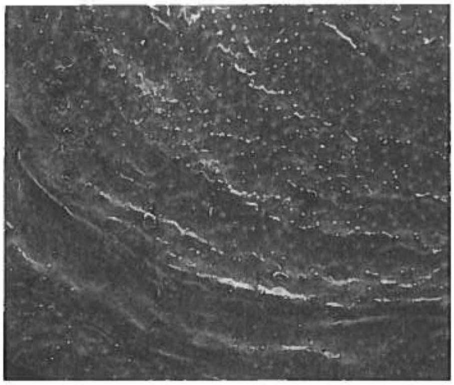

2c


3a


3b


1e


1f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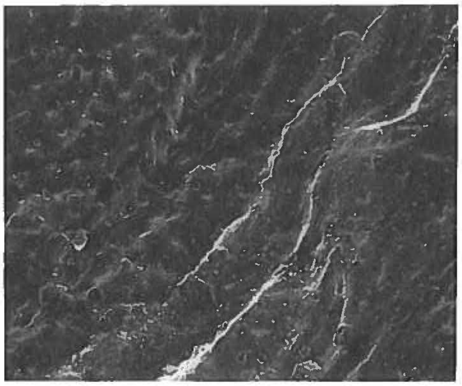

3d

Family Acrotretidae
Subfamily Acrotretinae

Genus *Canthylotreta* Rowell 1966

Type species. – *Acrotreta marjumensis* Walcott 1908, pp. 94–95, pl. 9, figs 2, 2a; by original designation.

Remarks. – The genus was known previously only from its type species, *C. marjumensis* (Walcott 1908), from the Great Basin of Utah and Nevada. In the western United States, this species occurs in the middle part of the *Cedaria* Zone. The new material from North Greenland does not extend the stratigraphic range of the genus but is referred to two species, *C. marjumensis* and the new species added here, *C. grada*.

Dorsal valves of *Canthylotreta* are similar to those of *Angulotreta* Palmer 1955, and *Apsotreta* Palmer 1955, but the dorsal median septum of *Canthylotreta* extends farther forward than it typically does in species of either of the other two genera. Furthermore, the outer surface of the dorsal valve has a noticeable sulcus in both species of *Canthylotreta*, a feature that is missing in species of *Angulotreta* and *Apsotreta*.

The ventral valve of *Canthylotreta* is not conical, as it typically is in *Angulotreta*, but it does resemble that of *Apsotreta* externally. The internal differences between these two genera, discussed previously in Rowell (1966), focus on the relationship of the internal pedicle opening to the apical process. In *Canthylotreta*, the opening lies entirely dorsal of the apical process; in *Apsotreta*, the pedicle passed through the thickened apex of the valve and emerged from a foramen within the apical process. The apical process of *Apsotreta* typically extends to near the middle of the valve and is much longer than that of *Canthylotreta*. It is possible that cladistic analysis would demonstrate that the two stocks are related and that a species of *Canthylotreta* is ancestral to the *Apsotreta* complex.

Canthylotreta marjumensis (Walcott 1908)

Fig. 10.7–10

1908 *Acrotreta marjumensis* – Walcott: 94–95, pl. 9: 2, 2a
1912 *Acrotreta marjumensis* (in part) – Walcott: 693, pl. 78: 2, 2b, 2c
1908 *Acrotreta ophirensis descendens* – Walcott: 95: pl. 9: 1 1a
1912 *Acrotreta ophirensis descendens* – Walcott: 698–699, pl. 78: 1, 1a-1c
1966 *Canthylotreta marjumensis* (Walcott) – Rowell: 5–9, pl. 1: 13–34

Material. – Nine ventral valves and 18 dorsal valves from GGU sample 271414. Approximately half of the valves are complete.

Remarks. – *Canthylotreta marjumensis* is a moderately variable species in the Great Basin of the western United States. The Greenland material is closely comparable to topotypic specimens from Utah, but differs in having a relatively higher ventral valve with an apex less strongly incurved over the ventral pseudointerarea. These differences are judged subjectively to be minor and the Greenland specimens are included in the taxon. Scanning electron microscope (SEM) examination showed that the circular, posteriorly directed pedicle foramen is confined entirely to the larval shell in the thickened beak (Fig. 10.8). The foramen caps the triangular, slightly concave pseudointerarea. Interiorly, the apical process is spatulate and prominent with thickened lateral margins. The internal pedicle opening is posterior and dorsal of the apical process and is flanked by two conspicuous apical pits. Anteriorly diverging *vascula lateralia* separate large, elliptical cardinal muscle scars from the apical process.

The triangular blade-like median septum in the dorsal valve reaches its maximum height at approximately 70 percent of the valve length. Posteriorly it buttresses a large, triangular, concave median plate that separates two anacline propareas along the posterior margin of the valve.

Occurrence. – *Canthylotreta marjumensis* is found in a single very fossiliferous sample (GGU 271414) of the Holm Dal Formation, 13 m from its base (Fig. 5).

Canthylotreta grada n. sp.

Fig. 9.1–5, 9

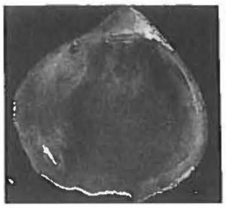
Holotype. – Ventral valve MGUH 18.024 from GGU sample 225547.

Fig. 8. *Orbithele* sp.

1–3. *Orbithele* sp. 1, juvenile dorsal valve exterior, in stereo view (a, b, X 27.5), and lateral oblique view (c; X 38.5); d, spine base on dorsal larval shell X 330; e, f, pitted ornament on larval shell (e, X 550; f, X 2200). MGUH 18.021 from GGU sample 225546. 2, ventral valve exterior, in stereo view (a, b) and lateral oblique view (c), all X 24.2. MGUH 18.022 from GGU sample 225546. 3, exterior of dorsal valve, larval valve with spines (a, X 44); b, ontogenetic change in shape shown by growth lines outside larval valve, X 19.8; c, d, detail of postlarval shell ornament (c, X 88; d, X 165). MGUH 18.023 from GGU sample 225547.


1a


2a


1b


2b


3


4


5


6a

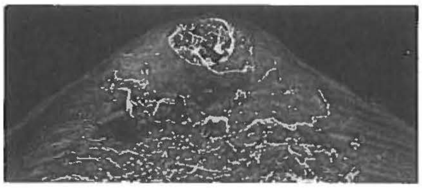

7a

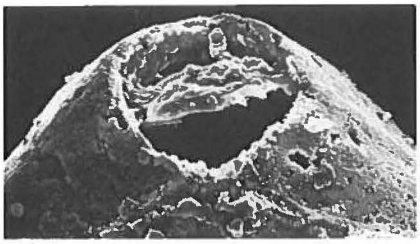

6b

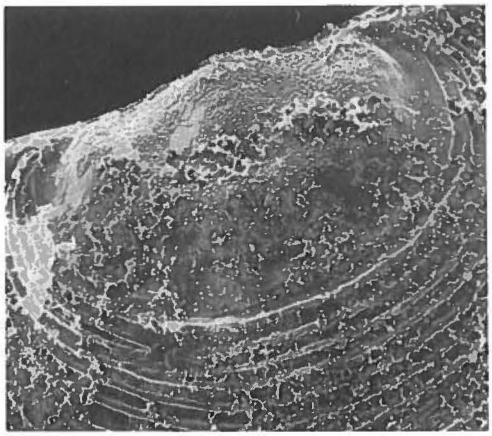

7b


8a


8b


1c


9


10

Additional figured material. – MGUH 18.025, 18.027, 18.028 from GGU sample 225547; MGUH 18.026, 18.029 from GGU sample 225540.

Material. – In all, 76 ventral and 60 dorsal valves from GGU samples 225540, 225546 and 225547. One broken but still articulated specimen was obtained from 225546. Most valves are fragmentary, but a few of the more robust dorsal and ventral valves are complete.

Diagnosis. – *Canthylotreta* with ventral valves that are catacline to gently apsacline and with thickening in apex not strongly developed.

Description. – Ventral valve catacline to apsacline, having convex lateral profile, only gently incurved beak. Foramen posteriorly directed, confined to larval shell (Fig. 9.1c), overhanging pseudointerarea with dorsally directed growth lines. Length and width of valve subequal; commissural outline rounded subtriangular, essentially straight posteriorly. Maximum height of valve about half length occurring near midlength of valve. Internally, cardinal muscle scars large, oval and anterolaterally directed. *Vascula lateralia* deeply incised (Fig. 9.la, b). Internal pedicle opening small, circular, flanked by slightly larger apical pits.

Dorsal valve transversely subtriangular to suboval in outline. Median sulcus extending back nearly to beak (Fig. 9.5). Concave median plate ornamented by fine growth lines separating small anacline propareas. Lateral commissural margin flattened in front of propareas. Median septum high, blade-like and subtriangular, extending forward almost to front of valve, maximum height of septum occurring about three quarters of valve length in front of beak, small median buttress at its posterior end. Short *vascula lateralia* diverging anterolaterally from front of buttress. Lobate cardinal muscle scars well developed, their posterior region beneath propareas (Fig. 9.2).

Remarks. – Although there is considerable variation within populations, *C. grada* may be distinguished from *C. marjumensis* by its more convex, less strongly apsacline ventral valve. Additionally, the beak of *C. grada* is less strongly incurved and its internal thickening, which is characteristic of *C. marjumensis*, is relatively weakly developed.

Occurrence. – The species occurs in the middle of the Holm Dal Formation (Fig. 3).

Genus *Prototreta* Bell 1938

Prototreta Bell 1938: 405; Bell 1941: 221–223; Shimer & Shrock 1944: 289; Goryanskij 1960: 178–179; Robison 1964: 559; Rowell 1965: 276–277; Aksarina in Aksarina & Pelman 1978: 60–61; Koneva 1979: 37–38

Homotreta Bell 1941: 230; Shimer & Shrock 1944: 289; Pelman 1977: 24

Type species. – *Prototreta trapeza* Bell 1938, p. 405, pl. 1, figs 1–6; by original designation.

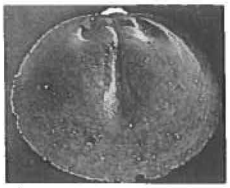
Remarks. – *Prototreta* and *Homotreta* are regarded here as subjective synonyms. Their ventral valves are essentially identical and the principal difference between the two genera is in the presence of a digitate septum in *Prototreta* in contrast to a simple, blade-like form in *Homotreta*. The two genera were established on mechanically prepared material and neither type species has been reinvestigated using acetic or formic acid treatment. Bell (1941) recognised that their two type species were isochronous homeomorphs and later considered that they should probably be regarded as synonyms (Bell & Ellinwood 1962). In at least two species of the related genus *Angulotreta* there are two phena, one with a simple septum, the other with a digitate structure (Palmer 1955, Bell & Ellinwood 1962). The significance of the digitation is unknown. It is unlikely to be an example of sexual dimorphism because both types of septa are not present in all populations.

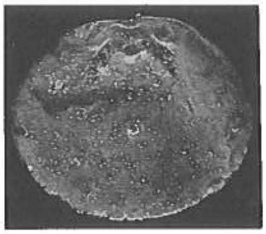
The genus *Prototreta* is known from the lower Middle Cambrian of North America and Rowell's unpublished data show it to range through the *Ptychagnostus punctuosus* Zone. Its presence in the Holm Dal Formation thus extends its range significantly. The majority of the North Greenland material is very fragmentary; only one species is described and even that is left in open nomen-

Fig. 9. *Canthylotreta grada* n. sp. and *Micromitra* cf. *M. modesta* (Lochman 1940)

1–5, 9. *Canthylotreta grada* n. sp. 1, holotype ventral valve, stereo view of interior (a, b, X 16.5) and posterior view of foramen and ventral pseudo-interarea (c, X 220). MGUH 18.024 from GGU sample 225547. 2, dorsal valve, stereo view of interior, (a, b, X 22). MGUH 18.025 from GGU sample 225547. 3, oblique lateral view of dorsal valve and septum, X 22. MGUH 18.026 from GGU sample 225540. 4, oblique lateral view of apsacline ventral valve, X 27.5. MGUH 18.027 from GGU sample 225547. 5, dorsal valve exterior with sulcus and noded beak, X 22. MGUH 18.028 from GGU sample 225547. 9, ventral valve foramen enclosed by larval valve, X 550. MGUH 18.029 from GGU sample 225540.
6–8, 10. *Micromitra* cf. *M. modesta* (Lochman 1940) 6, broken ventral valve exterior in stereo (a, b, X 22). MGUH 18.030 from GGU sample 225532. 7, dorsal valve exterior in stereo (a, b, X 27.5). MGUH 18.031 from GGU sample 225592. 8, detail of posterior margin of dorsal valve with thickened notothyrial margins and lack of homeochilidium (a, X 33) and featureless dorsal valve interior (b, X 17.5). MGUH 18.032 from GGU sample 225546. 10, detail of larval dorsal valve and immediately adjacent postlarval valve; note poorly defined nodes in larval valve and pitted micro-ornament, X 110. MGUH 18.033 from GGU sample 225592.


1a


2a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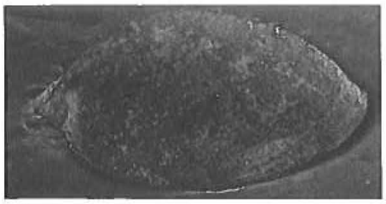
2b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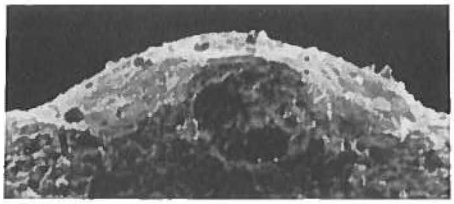
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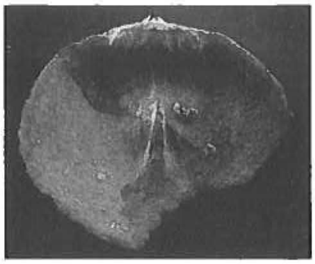
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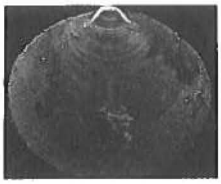
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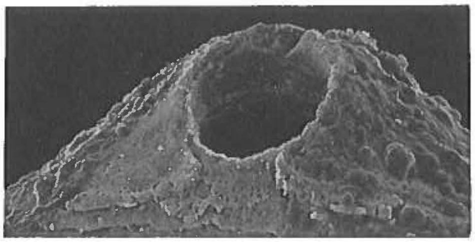
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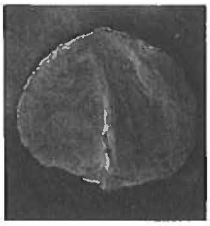
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clature. It is probable, however, that the genus is more widely distributed in the formation, for broken material, questionably referrable to *Prototreta*, occurs at several stratigraphic levels.

Prototreta sp.

Fig. 12.9–13

Material. – Twelve fragmentary ventral valves and 16 dorsal valves, only one complete, from GGU samples 225535 and 271414.

Description. – Low conical procline ventral valve; height averages 1.05 mm. Growth lines indicate valve transversely oval in commissural outline, posterior commissural margin straight. Well-defined intertrough on straight to slightly concave pseudointerarea capped by circular, posteriorly-directed foramen (Fig. 12.9). Anterior slope variable; straight to slightly concave or convex in lateral profile. Large internal pedicle opening on dorsal surface of apical process (Fig. 12.12b); bordered posterolaterally by apical pits. Deeply incised *vascula lateralia* diverge anterolaterally from pits (Fig. 12.12a). Cardinal muscle scars large, circular, lateral to apical pits.

Dorsal valve flat to gently convex and strongly sulcate; about 15 percent wider than long. Blade-like median septum triangular in lateral profile (Fig. 12.13). Long pseudointerarea (Fig. 12.10) with broad, triangular, depressed median plate flanked by smaller anacline propareas. Oval cardinal muscle scars extend anterolaterally from beneath pseudointerarea. Anterior and lateral portions of valve flattened to form brim that merges with propareas.

Remarks. – The material most closely resembles *Prototreta gorjanskii* (Pelman 1973). The principal difference is that the dorsal valve of the latter is much more strongly convex and lacks the conspicuous sulcus that is characteristic of the Greenland material. *Prototreta interupta* (Bell 1941) resembles specimens from the Holm Dal Formation in having a simple median septum, but the posterior margin of its dorsal valve is straight, rather than pointed and, furthermore, it has an unusual, beaded, fine ornament.

Occurrence. – *Prototreta* sp. was obtained from samples from the lower part of the Holm Dal Formation (Figs 3, 5).

Genus *Dactylotreta* Rowell & Henderson 1978

Type species. – *Dactylotreta redunca* Rowell & Henderson 1978, pp. 4–5, pl. 1, figs 1–8; by original designation.

Remarks. – *Dactylotreta* is characterised by its high procline to catacline ventral valve with the apical third or more of the valve occluded by an apical process. Within the genus, some species have a median dorsal septum, others lack one. In all known species, the median part of the dorsal pseudointerarea is buttressed.

Dactylotreta is a relatively widespread genus and is currently known from Australia, Antarctica and North America. In Australia, it ranges throughout much of the Upper Cambrian (Rowell & Henderson 1978), but in North America, Rowell's unpublished data show its first occurrence is in the upper part of the *Crepicephalus* Zone. The Holm Dal record thus extends the range of the genus slightly downward in this faunal province.

Dactylotreta patriella n. sp.

Fig. 11.1–5

Holotype. – Ventral valve MGUH 18.044 from GGU sample 225535.

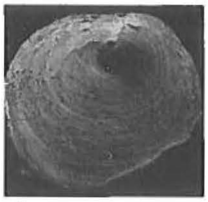
Other figured material. – MGUH 18.045–18.048 from GGU sample 225535

Material. – A total of 11 ventral valves and 5 dorsal valves from GGU sample 225535, all of which are abraded to some degree.

Fig. 10. *Linnarssonia tumida* Henderson & MacKinnon 1981 and *Canthylotreta marjumensis* (Walcott 1908)

1–6. *Linnarssonia tumida* Henderson & MacKinnon 1981. 1, ventral valve interior, in stereo (a, b, X 13.2). MGUH 18.034 from GGU sample 225586. 2, dorsal valve interior, in stereo (a, b, X 18.7). MGUH 18.035 from GGU sample 271414. 3, oblique lateral view of exterior of ventral valve X 16.5. MGUH 18.036 from GGU sample 225586. 4, ventral valve, posterior view of foramen and larval valve (a, X 275), and ventral interior with boss-like apical process (b, X 16.5). MGUH 18.037 from GGU sample 271414. 5, incomplete dorsal valve interior with large raised cardinal muscle scars X 16.5. MGUH 18.038 from GGU sample 271414. 6, dorsal valve interior X 11. MGUH 18.039 from GGU sample 271414.

7–10. *Canthylotreta marjumensis* (Walcott 1908). 7, dorsal valve interior, oblique lateral view (a, X 22) and in stereo (b, c, X 16.5). MGUH 18.040 from GGU sample 271414. 8, ventral valve, detail of foramen enclosed in larval valve (a, X 550) and interior view in stereo (b, c, X 27.5). MGUH 18.041 from GGU sample 271414. 9, ventral valve exterior, X 22. MGUH 18.042 from GGU sample 271414. 10, dorsal valve exterior, X 22. MGUH 18.043 from GGU sample 271414.



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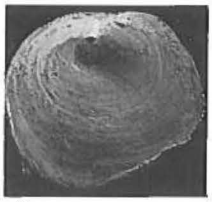

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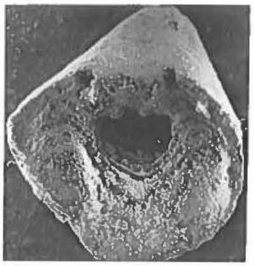

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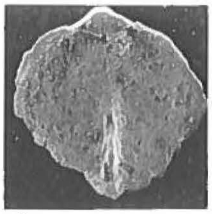

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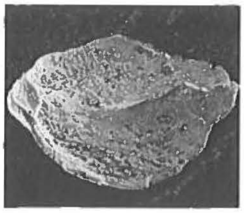

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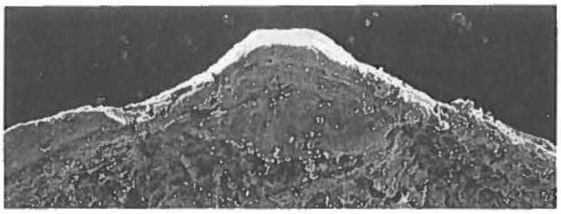

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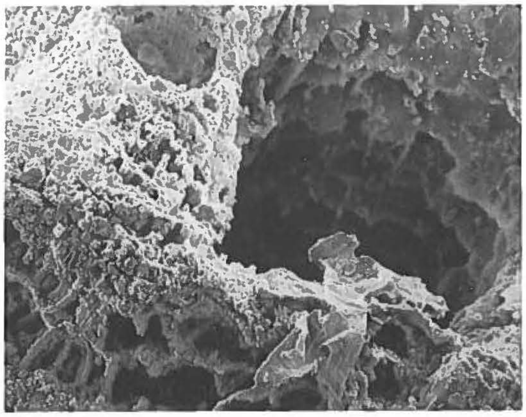

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Diagnosis. – *Dactylotreta* with ventral anterior slope planar to concave in lateral profile. Ventral pseudointerarea broad. Dorsal valve with low median septum and faint shallow sulcus.

Description. – Catacline ventral valve high conical, commissural outline slightly transversely oval. In lateral profile (Fig. 11.1c, d) anterior slope nearly straight apically, becoming markedly concave with growth. Fine growth lines present from base of larval shell to valve margin. Rounded beak with small circular, posteriorly directed foramen (Fig. 11.1e). Broad, well-defined, externally concave pseudointerarea, up to 50 percent of valve width. Internally, apical process occupies up to one third of valve height. Two small apical pits behind internal pedicle opening (Fig. 11.3a, b). Baculate *vascula lateralia* may be deeply incised.

Dorsal valve transversely oval; externally more convex posteriorly than anteriorly. Very shallow sulcus on anterior half of valve. Beak low, adjacent to commissural margin. Median septum low, maximum height approximately 100 µm immediately behind anterior terminous (Fig. 11.4c, d). Median plate small, concave, and triangular in outline, separating minute propareas that adjoin brim along posterolateral valve margin. Elliptical cardinal muscle scars extend anterolaterally from propareas.

Remarks. – *D. patriella* differs from both described species that have been referred to the genus in the slope of the anterior sector of the ventral valve. In the new species it is noticeably concave, whereas in both *D. redunca* (Rowell & Henderson 1978) and *D. solitaria* (Solov'ev et al. 1984), it is convex. The dorsal median plate of *D. patriella* is relatively shorter than that of *D. redunca*, and *D. solitaria* has a more prominent median buttress supporting this plate.

Occurrence. – The sample containing *Dactylotreta patriella* was taken 22 m above the base of the Holm Dal Formation (Fig. 3).

Subfamily Linnarssoniinae

Genus *Linnarssonia* Walcott 1885

Type species. – *Obolella transversa* Hartt in Dawson 1868, p. 644; by original designation.

Remarks. – The concept of the genus has had a rather checkered history. We are using it in the sense of Rowell & Henderson (1978) for a group of biconvex acrotretids whose apical processes are dominated by a high, subconical boss.

Linnarssonia tumida Henderson & MacKinnon 1981

Fig. 10.1–6

1981 *Linnarssonia tumida* – Henderson & MacKinnon: 301, figs 7K-P

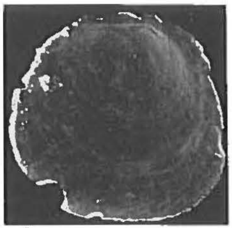
Material. – More than 800 specimens, most of which are fragmentary, from GGU samples 225532, 225540, 225546, 225567, 225586, 225592, 225595, 271403, 271414, and 271417.

Remarks. – Many of the species of *Linnarssonia* are in need of reexamination and revision. It is probable that there are many more available names than there are valid taxa. This topic and the potential synonomies involved are being investigated by our colleague, R. D. White.

The Greenland material is moderately variable but variability appears to be continuous and the collections are regarded as being samples of one species, *Linnarssonia tumida*. This species was discriminated by its authors from the common western North American taxon *Linnarssonia ophirensis* Walcott 1902, by its convexity and the relative height of its ventral pseudointerarea. *L.*

Fig. 11. *Dactylotreta patriella* n. sp.

1–5. *Dactylotreta patriella* n. sp. 1, holotype ventral valve in exterior stereo view (a, b, X 27.5, posterolateral view (c, X 27.5), oblique lateral view (d, X 22); e, posterior view of foramen, X 330. MGUH 18.044 from GGU sample 225535. 2, posterior view of ventral pseudointerarea, X 27.5. MGUH 18.045 from GGU sample 225535. 3, oblique view of fragmentary ventral valve apex showing posterior apical pits and extensive apical process, X 44. MGUH 18.046 from GGU sample 225535. 4, incomplete dorsal valve interior in stereo (a, b, X 24. 2); c, d, lateral view in stereo, X 27.5; e, detail of pseudointerarea, X 110. MGUH 18.047 from GGU sample 225535. 5, detail of shell ultrastructure in apical process, X 330. MGUH 18.048 from GGU sample 225535.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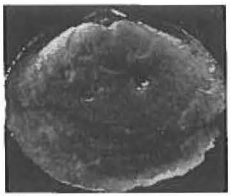
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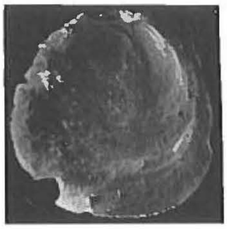
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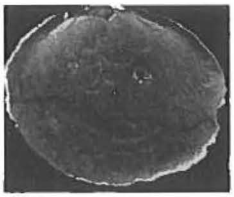
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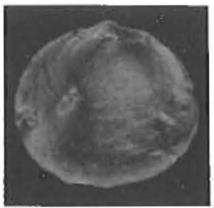
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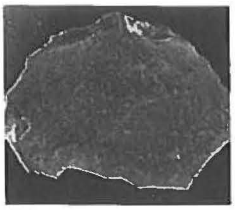
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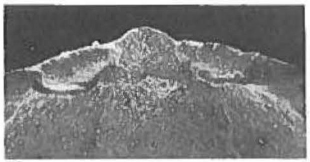
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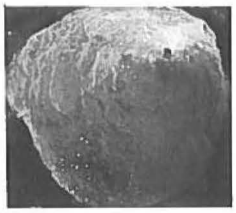
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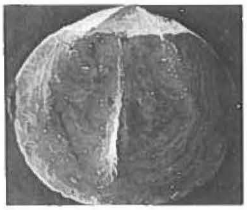
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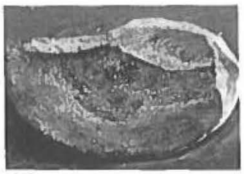
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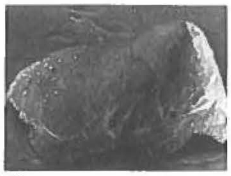
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ophirensis tends to have a more catacline ventral outline with maximum valve height near the beak. In contrast, *L. tumida* has a more rounded ventral lateral profile and the height of the pseudointerarea is about half the height of the valve. Comparison of topotypic material of these two species suggests that their dorsal valves are virtually indistinguishable.

Material from the Holm Dal Formation is closely comparable with topotypic specimens of *Linnarssonia tumida*. The most obvious difference is that the height of the ventral pseudointerarea of the Greenland material is higher in some specimens and varies between half and three-quarters of the valve height (Fig. 10.3). The Greenland specimens have a procline ventral valve whose pseudointerarea is externally slightly concave and bears a narrow intertrough. The external pedicle foramen is circular and posteriorly directed. SEM examination reveals that the foramen is not totally encircled by the larval shell (Fig. 10.4a), which bears the typical pitted ornament of the family. The ventral valve interior contains a prominent boss just anterior of the confluence of deeply-incised, baculate *vascula lateralia*. Two small ridges may diverge anterolaterally from the boss. The internal pedicle foramen is located posterior of the apical process and between large, subcircular cardinal muscle scars that are elevated above the valve floor.

The dorsal valve externally is more convex posteriorly than anteriorly. A small beak abuts the straight posterior margin. The interior of the dorsal valve also contains large, elevated, subcircular cardinal muscle scars; between them lies a short triangular median plate that in rare cases adjoins minute propareas. A low median ridge dominates the anterior slope of the valve and typically it extends forward between 60 and 70 percent of the valve length. Near the centre of the valve, a pair of small, elliptically bowed muscle scars are separated from it by *vascula media*.

Occurrence. – *Linnarssonia tumida* is rare to abundant in platy, mottled and brecciated limestones throughout the fossiliferous portion of the Holm Dal Formation.

Genus *Anabolotreta* Rowell & Henderson 1978

Type species. – *Anabolotreta tegula* Rowell & Henderson 1978, pp. 9–10, pl. 2, figs. 7–14.

Emended diagnosis. – Subequally biconvex shells, with procline, more rarely catacline ventral pseudointerarea. Apical process low, elongate, subtriangular in outline, grooved from crest to internal pedicle opening. Dorsal valve typically with short pseudointerarea, median ridge present, absent, or expanded as a median septum.

Remarks. – When the genus was erected, the only species known to belong to it had relatively simple dorsal valves that had either a very low median ridge or lacked one entirely. Subsequently, Rowell has collected specimens that belong to two, presently unnamed, taxa from the western United States. These forms have ventral valves closely similar to that of the type species, but their dorsal valves differ significantly from that of *A. tegula*. One of the groups has a dorsal valve with a well-developed median septum, that of the other bears a conspicuous median ridge. The emended diagnosis is needed to include them within the concept of the genus.

Anabolotreta groenlandica n.sp.

Fig. 13.1–7

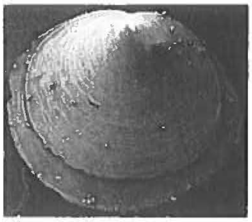
Holotype. – Ventral valve, MGUH 18.062 from GGU sample 225592.

Other figured material. – MGUH 18.063–18.065, MGUH 18.067 from GGU sample 271414; MGUH 18.066, MGUH 18.068 from GGU sample 225540.

Material. – A total of 44 ventral and 27 dorsal valves from GGU samples 225532, 225540, 225546, 225592 and

Fig. 12. *Curticia minuta* Bell 1944 and *Prototreta* sp.

1–8. *Curticia minuta* Bell 1938. 1, dorsal valve interior showing narrow propareas and median plate, in stereo (a, b, X 22). MGUH 18.049 from GGU sample 225592. 2, dorsal valve interior with faint impresions of cardinal muscle scars lateral of low median ridge, in stereo (a, b, X 22). MGUH 18.050 from GGU sample 225592. 3, ventral valve interior with gently apsacline propareas connected by collar, in stereo (a, b, X 33). MGUH 18.051 from GGU sample 225592. 4, ventral valve interior with well-developed propareas and collar, X 22. MGUH 18.052 from GGU sample 225592. 5, dorsal valve interior with weakly developed propareas and median plate, X 33. MGUH 18.053 from GGU sample 225592. 6, ventral valve fragment with very strongly developed triangular propareas, oblique interior view, X 44. MGUH 18.054 from GGU sample 225592. 7, oblique posterior view of ventral valve exterior with well-developed propareas that are scarcely visible from the outside, X 33. MGUH 18.055 from GGU sample 225592. 8, ventral propareas linked by strong collar, X 55. MGUH 18.056 from GGU sample 225592.
9–13. *Prototreta* sp. 9, ventral valve exterior, in stereo (a, b, X 16.5) and in oblique lateral profile (c, X 16.5). MGUH 18.057 from GGU sample 225535. 10, dorsal valve interior, stereo view (a, b, X 16.5). MGUH 18.058 from GGU sample 271414. 11, dorsal valve exterior, X 16.5. MGUH 18.059 from GGU sample 271414. 12, interior view of apical fragment of ventral valve showing pedicle opening, apical pits, and vascula lateralia (a, X 15.4), and detail of shell ultrastructure around apical process (b, X 110). MGUH 18.60 from GGU sample 225535. 13, oblique view into dorsal valve showing triangular profile of dorsal septum, X 16.5. MGUH 18.061 from GGU sample 271414.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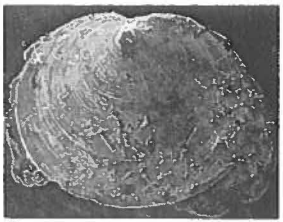
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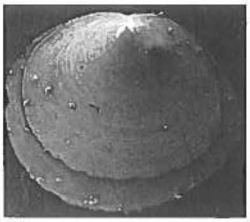
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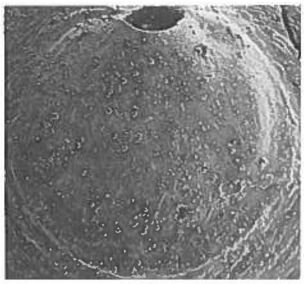
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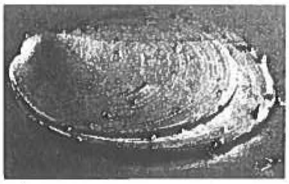
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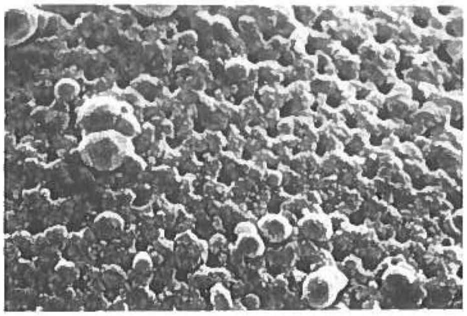
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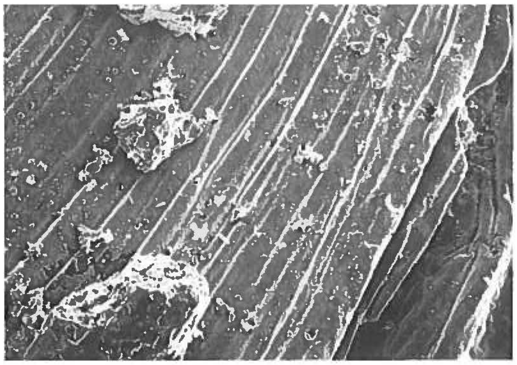
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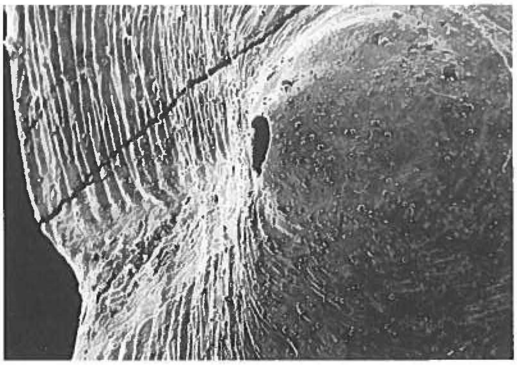
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271414. Very few of the valves are complete and unbroken.

Diagnosis. – *Anabolotreta* with subdued ornamentation. Ventral valve profile externally convex near beak, with concave anterior and lateral slopes. Dorsal valve with a variable low median ridge.

Description. – Shells about 20 percent wider than long, maximum width anterior of midline. Ornament of concentric growth lines and pronounced growth halts.

Ventral valve exterior convex near beak; anterior sector concave. Lateral portions of valve externally concave in anterior profile. Intertrough in procline pseudointerarea typically shallow, more rarely conspicuous. Beak with large circular, posteriorly-directed foramen. Ventral valve interior with low, anteriorly-broadening subtriangular apical process, grooved for approximately 60 percent of its length. Anterior margin of process well-defined; indistinct posterior margin abuts circular pedicle opening. Weakly impressed apical pits posterior to process. *Vascula media* between lobate cardinal muscle scars and apical process.

Dorsal valve predominantly convex, but posterolaterally flat to externally concave. Small triangular median plate, separating nearly imperceptible propareas. Subdued median ridge typically extends forward some 70 percent. Cardinal muscle scars suboval, in front of propareas. Anterior scars rarely preserved, but located anterolateral of median septum on low ridges.

Discussion. – *Anabolotreta groenlandica* differs from *Anabolotreta tegula* in its ventral exterior profile and also in the type of valve ornamentation. *A. tegula* is characterised by straight to slightly convex ventral anterior slopes, whereas the anterior and lateral slopes of *A. groenlandica* are decidedly concave. The well-developed exfoliation-type lamellae of *A. tegula* are not present in the new species, although shells of *A. groenlandica* may exhibit growth halts that resemble lamellae except that they are not undercut.

Occurrence. – *A. groenlandica* was obtained from limestones and limestone breccias throughout the fossiliferous part of the Holm Dal Formation.

Genus *Picnotreta* Henderson & MacKinnon 1981

Type species. – *Picnotreta debilis* Henderson & MacKinnon 1981, pp. 304–305, fig. 9H-P; by original designation.

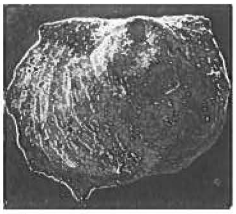
Remarks. – *Picnotreta* is a biconvex acrotretid genus characterised by having a strongly apsacline ventral valve with a pseudointerarea divided by a broadly triangular, externally concave median depression. The ventral beak is infilled with lamellose shell layers that are traversed by a very narrow pedicle tube. The apical process is variably developed and is typically more conspicuous in the type species than it is in undescribed North American forms that we would refer to the genus. The dorsal valve is morphologically less variable. The median plate of its pseudointerarea is weakly developed or absent, and is never supported by a median buttress. The median septum is a low triangular blade.

Picnotreta is most likely to be confused with *Acrothyra* Matthew 1901. Their dorsal valves are rather similar, but their ventral valves reveal clear differences; that of *Acrothyra* is linguloid in outline, and lacks the apical thickening found in *Picnotreta.* Because of the dorsal valve morphology, Henderson & MacKinnon (1981) referred *Picnotreta* to the Linnarssoniinae. We have followed them in the assignment, but with some reservations. If the genus is correctly placed, it is a relatively derived form and its lamellose apical thickening is seemingly an autapomorph.

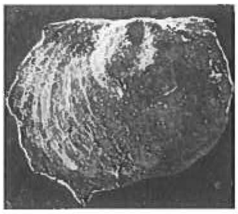
Picnotreta has a wide geographical distribution. It occurs in Australia and New Zealand (Henderson & MacKinnon 1981) and has been questionably identified in northern Victoria Land, Antarctica, (Rowell et al. 1984). In North America, presently undescribed specimens in Rowell's collections show that it ranges from the middle Middle Cambrian to within a few metres of the base of the Upper Cambrian *Aphelaspis* Zone.

Fig. 13. *Anabolotreta groenlandica* n. sp.

1–7. *Anabolotreta groenlandica* n. sp. 1, holotype ventral valve exterior showing prominent lamellae, in stereo (a, b, X 11); c, ventral larval valve X 110; d, oblique lateral view X 13.2; e, corroded pits in ventral larval valve, X 2750; f, detail of valve ornament, X 330; g, oblique view of larval valve and intertrough, X 110. MGUH 18.062 from GGU sample 225592. 2, ventral valve exterior, in stereo (a, b, X 22). MGUH 18.063 from GGU sample 271414. 3, dorsal valve interior, in stereo (a, b, X 13.2). MGUH 18.064 from GGU sample 271414. 4, broken dorsal valve exterior, in stereo (a, b, X 11). MGUH 18.065 from GGU sample 271414. 5, oblique lateral view of ventral valve exterior, X 66. MGUH 18.066 from GGU sample 225540. 6, oblique view into apex of ventral valve fragment showing apical process and form of internal pedicle opening, X 44. MGUH 18.067 from GGU sample 271414. 7, *vascula lateralia* in ventral valve interior, X 11. MGUH 18.068 from GGU sample 225540.

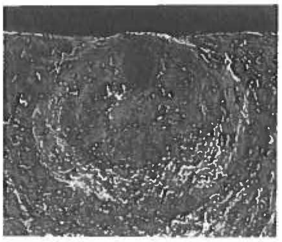

1a


2a


1b

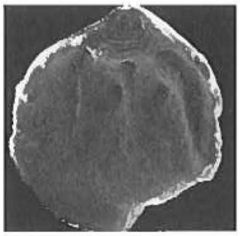

2b


3


1c


4

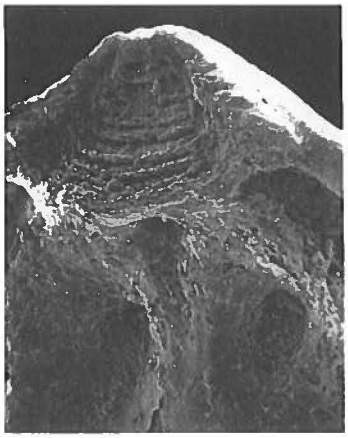

5a

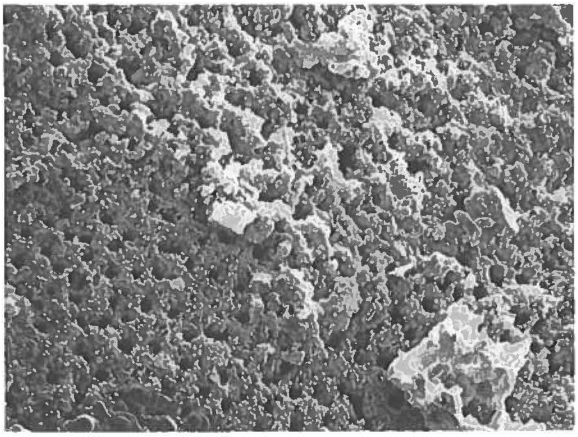

6a


7a


6b


7b


6c


5b

Picnotreta sp.

Fig. 14.4–7

Material. – Thirteen ventral valves and 3 dorsal valves from GGU sample 225535. Most of the specimens are fragmentary.

Remarks. – The Holm Dal material is very similar to specimens from the lower Upper Cambrian of the Great Basin of the western United States. It is not as well preserved, however, and consequently we are not creating a new taxon based upon it. The lamellose thickening of the beak is well developed and the thickening is traversed by a pedicle tube, whose internal opening lies immediately dorsal of the apical process (Fig. 14.6c). The apical process is considerably more subdued than that of *P. debilis*.

Occurrence. – *Picnotreta* sp. occurs near the base of the the Holm Dal Formation (Fig. 3). Three dorsal valves that are questionably referred to the genus were collected from near the top of the fossiliferous sequence.

Subfamily unassigned

Genus *Rhondellina* Rowell 1986

Type species. – *Rhondellina dorei* Rowell 1986, pp. 1061–1063, figs 1–5; by original designation.

Remarks. – A dorsibiconvex shell, lanceolate apical process, and exceedingly short ventral pseudointerarea make this acrotretid morphologically very distinctive. Features of the dorsal valve suggest that the genus is a very derived member of the Linnarssoniinae. The unusual shell microstructure is clearly different from that of other acrotretids, but is seemingly an autapomorph. In the absence of more information on the distribution of the type of shell ultrastructure, we prefer to leave the genus without formal subfamilial allocation.

Rhondellina dorei Rowell 1986

Fig. 14.1–3

1986 *Rhondellina dorei* – Rowell: 1061–1063, figs 1–5

Material. – Two ventral valves from GGU samples 225546 and 271414.

Remarks. – Although neither of the two known ventral valves is complete, they are almost identical to topotypic material from Nevada. The larval valve is slightly inflated and stands above the adjacent shell material. It completely encloses the pedicle foramen, which is continued anteriorly by a low groove (Fig. 14.1c). Internally, the lanceolate apical process extends forward from the internal pedicle opening as a low ridge. The shell microstructure is well preserved and shows the fine irregular ridges between inner shell lamellae that is characteristic of the taxon.

Occurrence. – *Rhondellina dorei* is very rare in limestones of the Holm Dal Formation (Figs 3, 5). In the United States, the species occurs in the *Crepicephalus* Zone, much higher stratigraphically than in Peary Land. Its presence in the Holm Dal Formation represents a significant downward extension of its range.

Family Curticiidae

Genus *Curticia* Walcott 1905

Type species. – *Curticia elegantula* Walcott 1905, pp. 319–320; by original designation.

Remarks. – We are following Rowell & Bell's (1961) concept of the genus, which was strongly influenced by their work on *Curticia minuta* Bell 1944. The stratigraphic range of the type species is seemingly limited, but *C. minuta* occurs through the *Cedaria* and *Crepicephalus* zones of the western United States.

Fig. 14. *Rhondellina dorei* Rowell 1986 and *Picnotreta* sp.

1–3. *Rhondellina dorei* Rowell 1986. 1, ventral valve exterior, in stereo (a, b, X 38.5); c, larval valve with elongate foramen, X 88. MGUH 18.069 from GGU sample 225546. 2, incomplete ventral valve, stereo of interior view showing elongate apical process (a, b, X 24.2). MGUH 18.070 from GGU sample 271414. 3, ultrastructure of ventral valve showing fibrous radial lamellae, X 440. MGUH 18.070 from GGU sample 271414.

4–7. *Picnotreta* sp. 4, dorsal valve interior X 33. MGUH 18.071 from GGU sample 225535. 5, ventral valve exterior view, X 18.7, and corroded larval valve surface, X 1100. MGUH 18.072 from GGU sample 225535. 6, incomplete ventral valve, interior view in stereo (a, b, X 33); c, pseudointerarea, internal pedicle opening and apical pits, X 110. MGUH 18.073 from GGU sample 225535. 7, ventral valve interior, stereo view (a, b, X 22). MGUH 18.074 from GGU sample 225535.

Curticia minuta Bell 1944

Fig. 12.1–8

1944 *Curticia minuta* – Bell in Lochman & Duncan: 145–146, pl. 18: 21–32
1961 *Curticia minuta* – Rowell & Bell: 928–929, pl. 104: 1–20

Material. – The species is abundant in GGU sample 225592 and also occurs in samples 225540, 225544, 225546, and 225595. The collections include about 200 specimens, but the majority are broken valves.

Remarks. – *Curticia minuta* is a small, ventribiconvex species of the genus; typically, it is only a third or less of the maximum size of the type species. In external shape, the Greenland material agrees closely with *C. minuta* described from its type area in Montana (Bell 1944, Rowell & Bell 1961). The species is unusually variable in its internal features. Rowell & Bell (1961) illustrated differences in development of the dorsal pseudointerarea from a single sample and discussed changes in the shape of the pedicle opening both during ontogeny and among comparably sized adults. The Greenland specimens differ from those in the Montana collections by having much smaller dorsal pseudointerarea: that shown in Fig. 12.1 is typical. The dorsal propareas are short, and although the intervening median plate is wide, it does not extend forward very far. The ventral propareas of the Holm Dal material are less variable than those from Montana but, nevertheless, there is a considerable diversity in them and in the shape of the pedicle opening. The external lateral margin of the pseudointerarea, and thus of the propareas, is well defined by an abrupt flexure of the shall material (Fig. 12.6). These margins intersect just below the beak of the ventral valve and bound an angle typically of about 120 degrees. The angle varies considerably between individuals, having an approximate range of 90 to 150 degrees. When viewed externally, the pedicle opening is triangular and bounded by these margins (Fig. 12.7); because of the apsacline inclination of the posterior margin, the propareas are scarcely visible in such a view. In commissural view, however, the propareas are seen to be basically triangular plates, inset in front of the pedicle opening and joined apically by a variably developed collar (Fig. 12.3, 6, 8). The plates are apsacline and typically ornamented by growth lines parallel to their dorsal margin.

Occurrence. – *C. minuta* occurs in limestones in the middle of the Holm Dal Formation (Figs 3, 6). These occurrences are among the oldest known for the taxon.

Order Paterinida
Superfamily Paterinacea
Family Paterinidae

Genus *Micromitra* Meek 1873

Type species. – *Iphidea sculptilis* Meek 1873, p. 479; by original designation.

Remarks. – Systematic relations among the paterinids are still poorly understood and the group is in need of monographic treatment. We are using the concept of *Micromitra* in the sense of Rowell (1965) for relatively thick-shelled paterinids with strong concentric fila, with or without the development of a reticulate pattern formed by intersection of the fila with radial costellae. The genus ranges through much of the Middle and Upper Cambrian.

Micromitra cf. *M. modesta* (Lochman 1940)

Fig. 9.6–8, 10

1940 *Paterina modesta* – Lochman: 14, pl. 1: 20–21
1940 *Micromitra paucicostellae* – Lochman: 14–15, p. 1: 23–24
1944 *Micromitra modesta* (Lochman) – Bell in Lochman & Duncan 1944: 144–145, pl. 18: 1–8, 18, 19
1960 *Micromitra modesta* (Lochman) – Lochman & Hu: 820, pl. 95: 37–40
1964 *Micromitra modesta* (Lochman) – Robison: 56, pl. 92: 1–4
1965 *Micromitra modesta* (Lochman) – Grant: 96, pl. 8: 3–4

Material. – The material consists of 10 small valves and several fragments from GGU samples 225532, 225546, and 225592.

Remarks. – The type material consists of valves that were mechanically extracted from the enclosing matrix and which are about twice the size of the Greenland specimens. The largest individuals from the Holm Dal Formation are just over 1 mm in length and are probably juveniles. In their gross shape and in the strong development of concentric ornament they resemble *M. modesta*, but differ from it in lacking a homeochilidium. Absence of this structure is characteristic of early developmental stages in other paterinids. The etched material reveals little of internal features except the pronounced shell thickening along the margins of the notothyrium (Fig. 9, 8). The early-formed larval shell bears two poorly defined nodes and is ornamented by a microreticulation that defines small shallow pits in the valve surface (Fig. 9.10). The latter feature has not been observed previously in paterinids and consequently its distribution within the order is unknown.

Occurrence. – *Micromitra* cf. *M. modesta* occurs sporadically throughout the fossiliferous part of the Holm Dal Formation (Figs 3, 6).

Order Lingulida
Superfamily Lingulacea
Family Obolidae

Genus *Lingulella* Salter 1866

Type species. – *Lingula davisii* M'Coy 1851, pp. 405–406; by subsequent designation, Dall 1870, p. 159.

Remarks. – Although the number of available names for lingulacean genera has more than doubled since the last summary of the superfamily (Rowell 1965), the genus *Lingulella* remains a 'catch-all' name for elongate obolids. As Krause & Rowell (1975) have observed previously, it is relatively easy to see how the situation has arisen. With few exceptions, lingulaceans are externally rather featureless and only rarely do their shells possess complex internal structures. The type species of *Lingulella,* however, differs from many species that have been referred to the genus because the visceral area of both valves is strongly pitted (e.g. Rowell 1965, fig. 161: 3a,c,d). The functional significance of this pitting, if any, is unknown. It is developed in one of the three species found in the Holm Dal Formation. The most abundant species in the formation, here termed *Lingulella* sp. 1, lacks these pits and also differs in the structure of its pseudointerareas from typical *Lingulella*. It can be referred to the genus only by using a very broad generic concept. The available material, however, does not merit creation of a new taxon to receive it.

Lingulella sp. 1

Fig. 15.1, 2, 5, 7

Material. – Approximately 200 specimens belonging to this form have been collected. The majority are from GGU sample 225592, but it occurs also in GGU samples 225540, 225542, 225544, 225547, 225593, 225595, 271403, 271414, and 271417.

Remarks. – This is the common lingulacean in the Holm Dal Formation. Individuals are moderately large with a maximum observed length of about 7 mm. When juvenile, shells are elongate suboval in commissural outline, but as adults they become subacuminate with rounded anterior margins. The shells are unusual in the family in that they are strongly biconvex and the ventral valve is only slightly longer than the dorsal one. Internally, the valves are rather featureless except for their pseudointerareas; these differ rather markedly from typical *Lingulella* but, to our knowledge, are unlike those of any described obolid. The dorsal propareas are narrowly triangular and are connected by a median plate that is approximately orthocline but lies slightly dorsal of the commissural margin and projects forward as a shelf (Fig. 15.2). Their ventral propareas are also approximately orthocline but, in the few specimens that preserve this part of the valve, they seemingly differ from typical *Lingulella* in that they are not connected by a pedicle groove (Fig. 15.5). This form occurs throughout the formation.

Lingulella sp. 2

Fig. 15.4

Material. – Three incomplete valves from GGU sample 225535.

Remarks. – The preserved features of the valves are consistent with the material being *Lingulella* in its restricted usage. The visceral area of each valve is strongly pitted (Fig. 15.4); the dorsal propareas are approximately orthocline and are joined by a median plate that is depressed and adnate to the posterior inner surface of the dorsal valve.

Lingulella sp. 3

Fig. 15.3, 6, 8.

Material. – Fourteen valves from GGU samples 225544, 225546, 271408, 271414, 315007, 315011, including the figured specimens.

Remarks. – In commissural outline, these valves are similar to those of *Lingulella* sp. 1 except that they are slightly wider and considerably less convex. The ventral pseudointerarea is unknown, but the dorsal pseudointerarea differs from that of *Lingulella* sp. 1 in possessing propareas and an adnate median plate; it is thus comparable to that of *Lingulella* in a restricted sense. The visceral areas of *Lingulella* sp. 3, however, lack pits. The species ranges throughout the Holm Dal Formation.

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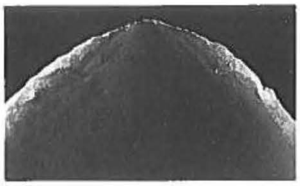
1a


2a


1b


2b


3a


3b


4a


5a

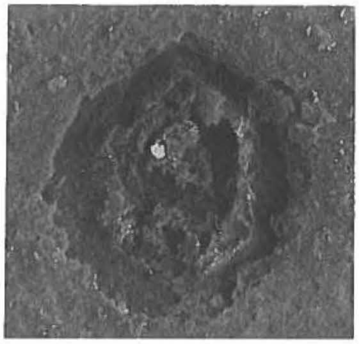

4b


5b


6


7a


8


4c


7b

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Fig. 15. *Lingulella* spp. 1–3

1, 2, 5, 7. *Lingulella* sp. 1. 1, stereo view of articulated valves, dorsal valve uppermost (a, b, X 13.2). MGUH 18.075 from GGU sample 225592. 2, dorsal valve interior with shelf-like pseudointerarea, stereo view (a, b, X 11). MGUH 18.076 from GGU sample 225592. 5, ventral valve interior, stereo view (a, b, X 7.7). MGUH 18.077 from GGU sample 225592. 7, ventral valve exterior (a, X 13.2) and detail of valve ornament (b, X 88). MGUH 18.078 from GGU sample 225592.

4. *Lingulella* sp. 2. 4, interior of dorsal valve fragment, stereo view (a, b, X 12.1); c, detail of internal pit on visceral area X 220. MGUH 18.079 from GGU sample 225535.

3, 6, 8. *Lingulella* sp. 3. 3, dorsal valve propareas and low median ridge, stereo view (a, b, X 12.1). MGUH 18.080 from GGU sample 225544. 6, dorsal valve exterior, X 4.4. MGUH 18.081 from GGU sample 225594. 8, ventral valve exterior, X 3.9. MGUH 18.082 from GGU sample 225594.

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Peel, J. S. Molluscs of the Holm Dal Formation (late Middle Cambrian), central North Greenland. Meddr Grønland, Geosci. 20: 145–168. Copenhagen 1988–12–31.

A small, but diverse fauna of molluscs is described from the lower beds of the Holm Dal Formation (late Middle Cambrian) of central North Greenland. Species of Helcionellacea and Hypseloconellacea dominate, although only individuals of the former superfamily are numerically common, as are examples of a single stenothecoid species. Paragastropoda and Hyolitha are rare faunal elements. A single new genus *(Perssuakiella)* and 5 new species are described: *P. troelseni, Latouchella holmdalense, L. pearylandica, Stenothecoides groenlandica and Costipelagiella kochi.*

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Molluscs are a generally uncommon element within the fauna of the Holm Dal Formation (late Middle Cambrian) of central North Greenland (Fig. 1). Less than fifty specimens are available for study from grainstones in the lower part of the formation, compared with the many hundreds of specimens of both trilobites and brachiopods described elsewhere in this volume (Robison; Zell & Rowell). In terms of diversity, however, the discrepancy is less strongly marked. Thirteen molluscan species are recognised, compared with 14 species of inarticulate brachiopods and 58 species of trilobites (Figs 2–4). Many of the molluscan taxa are known only from single specimens; taking into account the effects of variable preservation this has often resulted in such material being described in open nomenclature.

Most of the Holm Dal molluscs are simple cap-shaped, or isostrophically coiled univalves which can be referred to the Class Monoplacophora Knight 1952. In recent years, however, the scope of this taxon has been subject to so much debate that it can not be employed meaningfully without qualification as to content (compare Runnegar & Jell 1976, Yochelson 1979; Runnegar & Pojeta 1985; Salvini-Plawen 1985; Wingstrand 1985; Geyer 1986). Thus, the term is not employed in the present context and relevant taxa are assigned either to the Superfamily Helcionellacea or to the Superfamily Hypseloconellacea.

The molluscan fauna of the Holm Dal Formation is unusual in that it contains representatives of both Helcionellacea and Hypseloconellacea. Members of the latter superfamily are typical of Upper Cambrian inner shelf sequences, particularly in central North America (Berkey 1898; Stinchcomb 1986). They are not commonly associated with Helcionellacea, individuals of which are more characteristic of Lower and Middle Cambrian strata. The association of members of the two superfamilies confirms the late Middle Cambrian age (*Lejopyge laevigata* Interval-zone of the Swedish standard zonation; early Dresbachian of much of North America) suggested on the basis of the trilobite faunas by Robison (this volume).

Relatively few studies exist of molluscs of Middle and Late Cambrian age, although a number of taxa have been recorded as minor elements of trilobite-dominated faunas. Few of these taxa are adequately described or illustrated, causing difficulties in the comparison of Holm Dal molluscs with published literature. Exceptions are provided by recent studies of Middle Cambrian molluscs from Australia (Runnegar & Jell 1976), Spain and Marocco (Geyer 1986) and a large Upper Cambrian fauna from the Antarctic (Yochelson et al. 1973; Webers et al. in press). A sequence of papers by Stinchcomb (1975, 1980, 1986, see also Stinchcomb & Echols 1966) has illuminated problems associated with hypseloconellacean-dominated faunas of Late Cambrian to Early Ordovician age in Missouri. Unfortunately, only material from the latter study shows more than slight similiarity to the Holm Dal fauna.

In view of the paucity of described contemporaneous material, it is not unexpected that little relationship can be established between the molluscan fauna of the Holm Dal Formation and faunas from other areas. A single taxon of uncertain generic position compares well with a Dresbachian species from the Missouri area (*Kiringella? washingtonense* Stinchcomb 1975).

Repositories. – Type and figured specimens are deposited in the type collection of the Geological Museum, Copenhagen, Denmark (MGUH prefix). Other material is retained in the collections of the Geological Survey of Greenland, Copenhagen (GGU prefix).

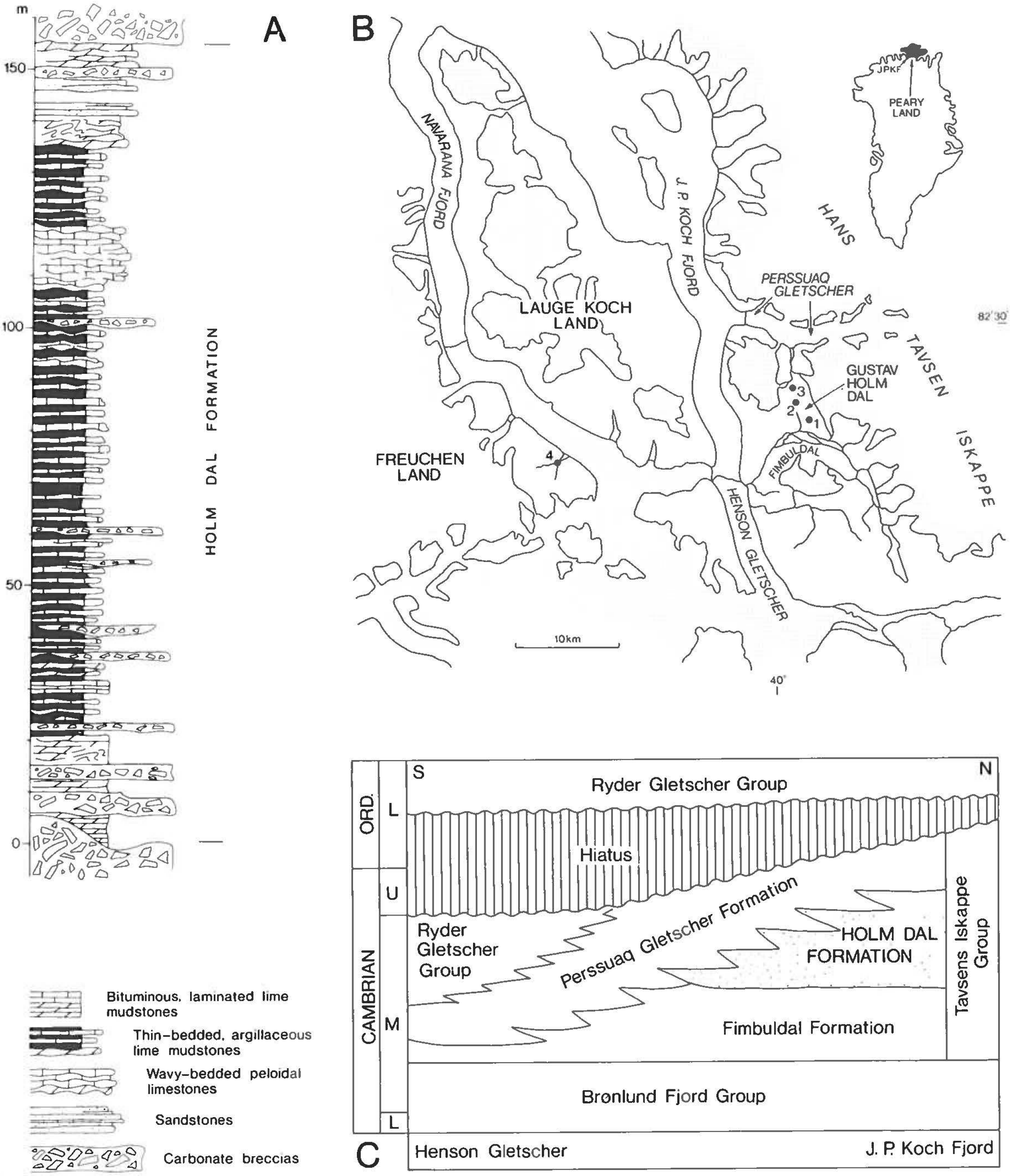

Fig. 1. Derivation of molluscs from the Holm Dal Formation, central North Greenland. A, stratigraphic section through the Holm Dal Formation at its type locality (locality 1 in Fig. 1B; from Ineson this volume). B, map of the area around Gustav Holm Dal, westernmost Peary Land, central North Greenland. 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 locality (Fig. 1A) and adjacent area, GGU collections in the sequence 225528–225567; 2, east side of Gustav Holm Dal, GGU collections 225586, 271403, 271404, 271408, 271414, 271417; 3, east side of Gustav Holm Dal, GGU collections 225592–225595; 4, south-east Freuchen Land, GGU collections 315007, 315009, 315011–315013. Not all collections and localities have yielded molluscs. C, stratigraphic relationship of the Holm Dal Formation (from Ineson, this volume).

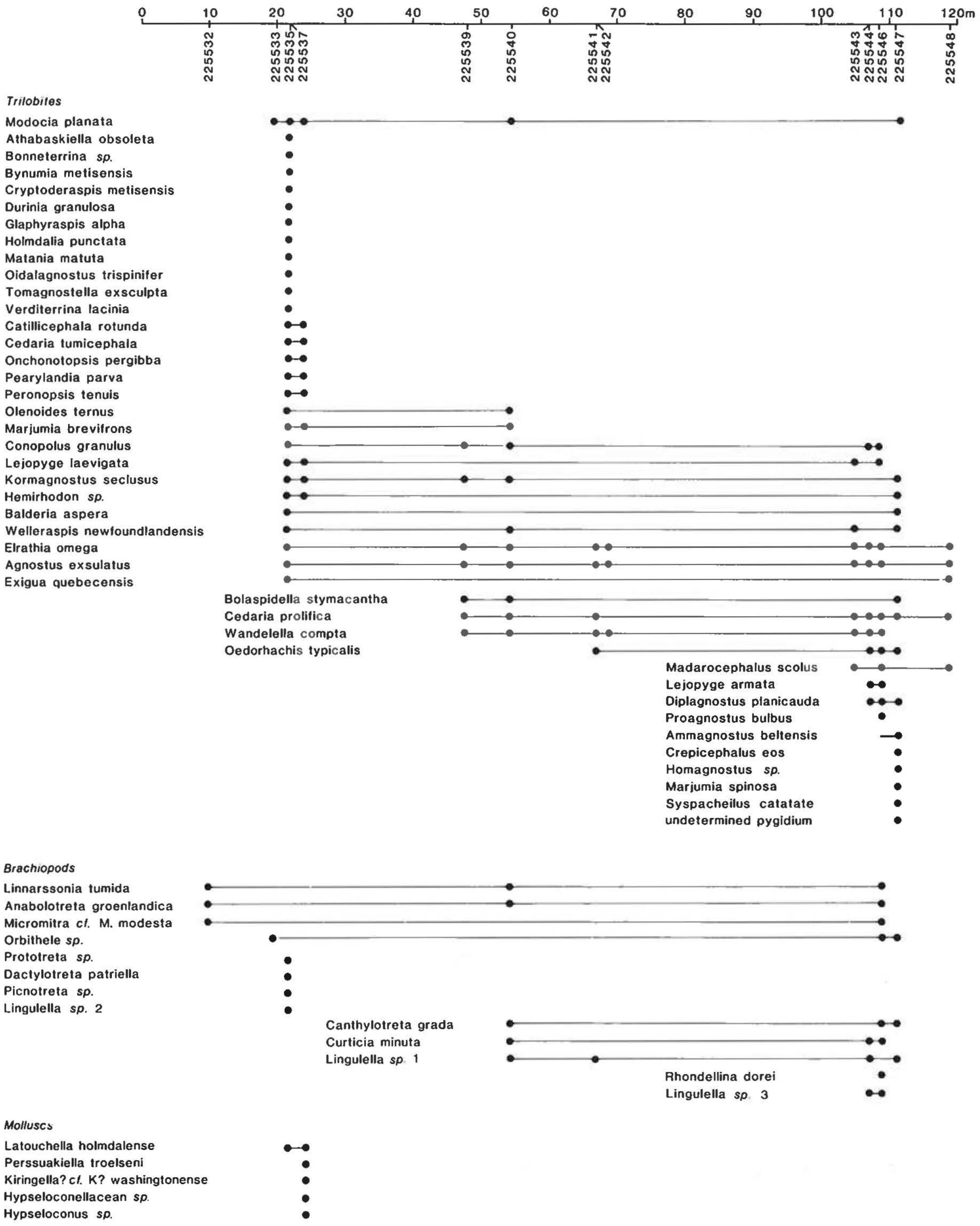

Fig. 2. Stratigraphic distribution of trilobites, brachiopods and molluscs from the type section of the Holm Dal Formation (Fig. 1A, locality 1 in Fig. 1B). Six-digit numbers are GGU collection numbers. The formation is almost 155 m thick in its type section; scale indicates height above base of formation.

	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. Trilobites, brachiopods and molluscs in GGU collections from the lowest part of the Holm Dal Formation in the vicinity of the type section (see Figs 1, 2). Collections are not in stratigraphic sequence.

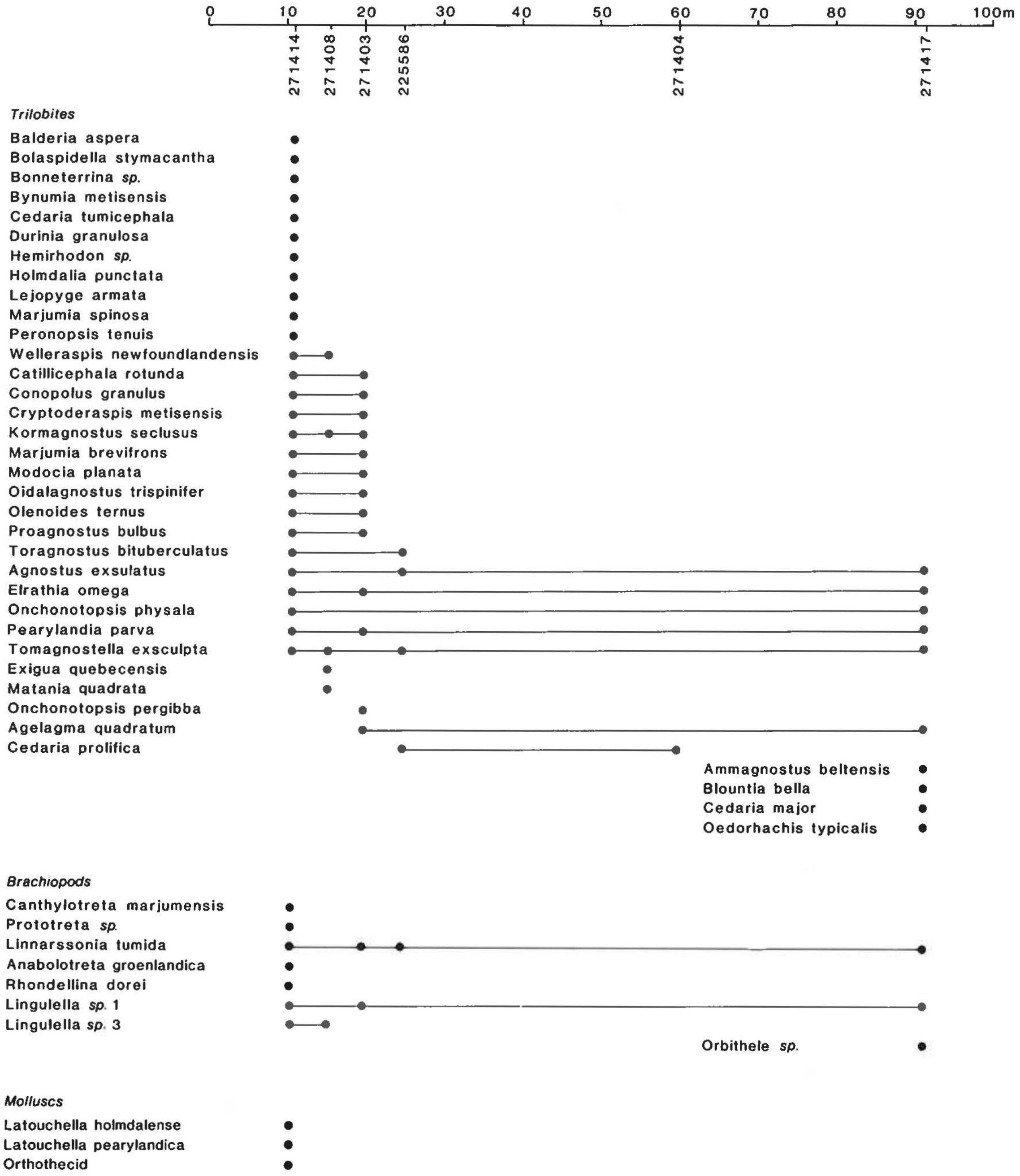

Fig. 4. Stratigraphic distribution of trilobites, brachiopods and molluscs in GGU collections (six-digit numbers) from locality 2 (Fig. 1B) of the Holm Dal Formation. Scale indicates height above the base of the formation.

Stenothecoida

Members of this group are bivalved, with closely fitting calcareous valves, although specimens with conjoined valves are infrequent. At different times considered to be crustaceans, bivalves or univalved molluscs, they are best placed as a separate class within the Mollusca, the Stenothecoida Yochelson 1968 (= Probivalvia Aksarina 1968; see Yochelson 1969, also Rasetti 1954; Horny 1956; Robison 1964; Koneva 1976).

Stenothecoids are often considered to be very variable in form and this variability may explain the wealth of species recognised in certain studies (e.g. Koneva 1979). Certainly the Holm Dal material described here as a single species includes morphs which elsewhere might be assigned to several taxa.

Genus *Stenothecoides* Resser 1938

Type species. – *Stenotheca elongata* Walcott 1884 (in part)

Stenothecoides groenlandica n. sp.

Figs 5, 6

Derivation of name. – After Grønland (Danish, Greenland).

Holotype. – MGUH 18.671 from GGU collection 225552, illustrated as Fig 5A, H, I

Material. – Fifteen specimens from GGU collections 225528, 225529, 225552, 225561, 225563, 225564 (Fig. 3).

Description. – A species of *Stenothecoides* in which the individual valves vary from about three-quarters as wide as long (Fig. 5A) to less than half as wide as long (Fig. 6A, C). Individual valves may be almost bilaterally symmetrical in young specimens (Fig. 5E) but larger examples are often clearly asymmetric. Apex marginal or slightly overhanging the adapical margin, varying from strongly curved to left or to right in apical view (Fig. 5G) but mainly almost symmetrical; forming the initial, most prominent end of a ridge or fold of variable expression which extends to the abapical margin. In plan view the individual valves tend to be most pointed adapically; greatest width is generally achieved at about one third to one half of the length, viewed in plan view and measured from the adapical margin (Figs 5A, 6C, 6D). Commonly, one abapico-lateral apertural margin is excavated relative to the other in plan view (compare the left and right sides in Figs 5A, 6C). Commissure apparently flat, lying within a single plane. In abapical view, the valves vary from convex to sub-triangular in cross-section (Fig. 5C), although the median dorsal angulation is usually prominent. Shell thick, with irregularly developed growth lines.

Discussion. – Bivalved specimens of the type described by Yochelson (1969, figs 1, 2), Aksarina & Pelman (1978, pl. 17) and Koneva (1979, pl. 3: 1, pl. 5) have not been observed. Hence, the distinction employed by Yochelson between ventral and dorsal valves, with a horizontal commissure, can not be certainly applied. Illustrations given by Yochelson (1969, fig. 2) of *Stenothecoides knighti* from the Lower Cambrian of the Yukon of conjoined valves in apical view show the apices turned to the left, i.e. the dorsal valve curves anticlockwise during growth (in dorsal plan view) and the ventral valve curves clockwise (in ventral plan view). This curvature is also seen in Siberian specimens illustrated by Yochelson (1969, fig. 1). Assuming that the same direction of curvature is present in *Stenothecoides groenlandica,* both the valves illustrated in Fig. 5F, G would be interpreted as ventral. Strong curvature with growth, however, is not a feature of most valves.

Koneva (1976) favoured orientation of stenothecoids as bivalves, with the plane of contact between the valves oriented vertically in contrast to the horizontal orientation suggested by Yochelson (1969). Apices in *Bagenovia kazakhstanica* Koneva 1976 from the Lower Cambrian of Kazakhstan, are stated to be occasionally prosogyral. In this interpretation, both the illustrated valves in Fig. 5F, G would be left valves.

Stenothecoides knighti Yochelson 1969 is distinguished from *S. groenlandica* by its well-rounded adapical margin and uniformly oval plan (cf. Yochelson 1969, fig. 2A, B). In *S. groenlandica* the adapical margin is more acute and adults are commonly almost diamond-shaped in plan. *S. labradorica* Resser 1938 from the Lower Cambrian of eastern Canada, as described by Rasetti (1954: 65, pl. 11: 1, 2) is much narrower than typical *S. groenlandica.* The unusually narrow example of *S. groenlandica* illustrated as Fig. 6A-C is differentiated from *S. labradorica* in being less acute adapically, with maximum shell width at about one third, of the length: in *S. labradorica* maximum width is achieved first at half the length.

Stenothecoides elongata (Walcott 1884), redescribed by Rasetti (1954, see also Robison 1964) is more slender and uniformly oval in plan than adult *S. groenlandica*; the species is reminiscent of the juvenile *S. groenlandica* (Fig. 5E) but this is less pointed adapically.

Aksarina & Pelman (1978) described several new genera and species of Stenothecoida from the Lower Cambrian of Siberia. Most are more slender than *S. groenlandica.* Some of the cambridiids (e.g. *Bagenovia* Horny 1956 and *Katunioides* Aksarina in Aksarina & Pelman 1978) are characteristically wide and crudely

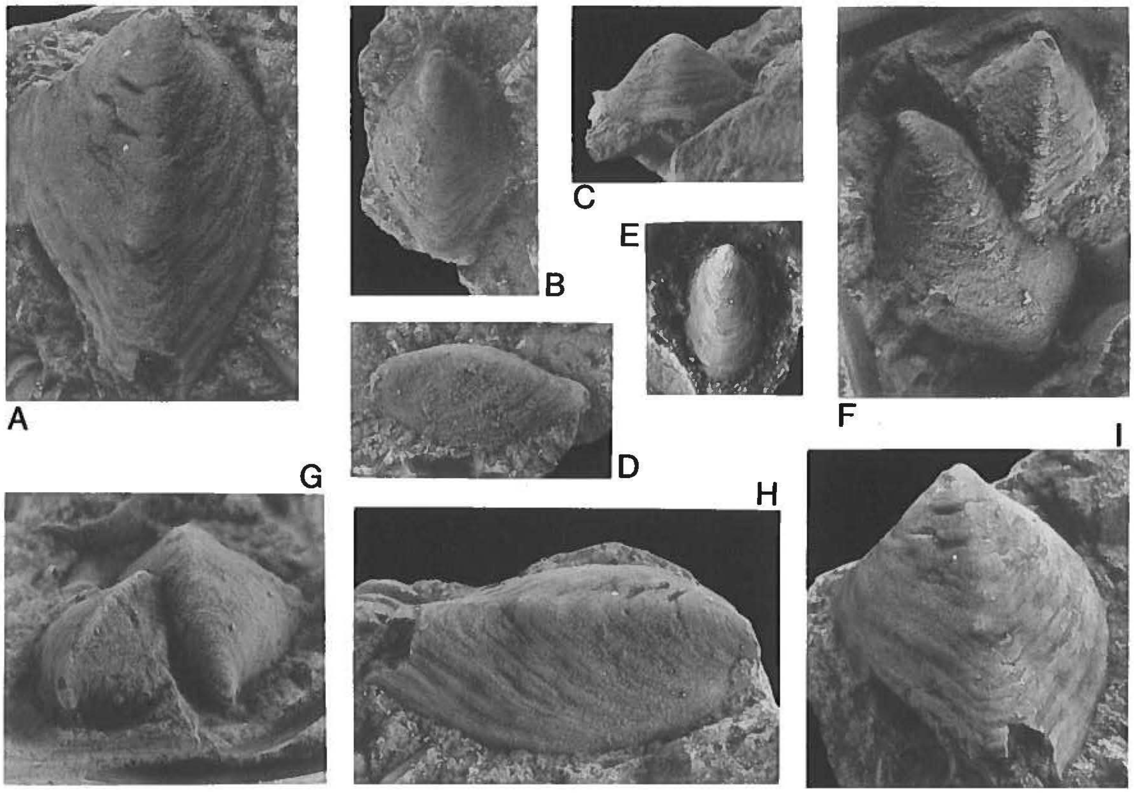

Fig. 5. *Stenothecoides groenlandicus* n. sp.
A, H, I, MGUH 18.671, holotype, from GGU collection 225552, plan, oblique lateral and oblique abapical views of the valve, very slight twisting suggests that this may be a right valve, although the apex is damaged, X 6.6. B, C, D, MGUH 18.672 from GGU collection 225529, plan, abapical and oblique lateral views of an almost symmetrical valve; slight apical twisting suggests that this may be a left valve, X 6.6. E, MGUH 18.673 from GGU collection 225561, juvenile valve, X 6.6. F. G, MGUH 18.674 and 18.675 from GGU collection 225552, plan and apical views of two supposed left valves, X 6.6.

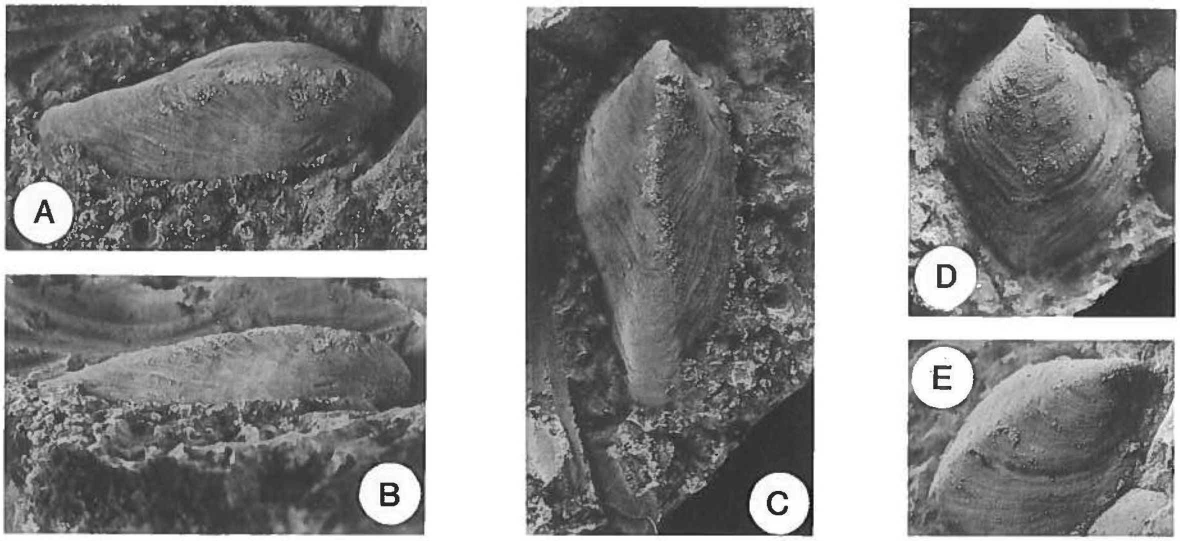

Fig. 6. *Stenothecoides groenlandicus* n. sp.
A-C, MGUH 18.676 from GGU collection 225561, oblique-lateral, lateral and plan views of an unusually narrow, possible right valve, X 6. D, E, MGUH 18.677 from GGU collection 225552, plan and oblique abapico-lateral views, X 6.

diamond-shaped in plan view, but are readily distinguished from *S. groenlandica* by their high shells with a prominent pointed apex. Koneva (1979) described many new stenothecoid species mainly from the Lower Cambrian of Kazakhstan, although it is difficult to assess variation within this material. Several of these species are carinate and thus reminiscent of *S. groenlandica;* they differ in being more pointed adapically.

Helcionellacea

Runnegar & Jell (1976) employed a much wider concept of this monoplacophoran superfamily than that envisaged by Knight et al. (1960), where the Helcionellacea Wenz 1938 was regarded as a superfamily within the Archaeogastropoda. They recognised 7 constituent families, including the Hypseloconidae Knight 1956, although this family is here excluded from the Helcionellacea and placed within the Superfamily Hyseloconellacea Knight 1956, as advocated by Stinchcomb (1986).

Following interpretations of *Yochelcionella* and *Oelandia* proposed by Geyer (1986) and Peel & Yochelson (1987), helcionellaceans are considered to be untorted, endogastrically coiled molluscs which are not closely related to the untorted, exogastrically coiled tryblidians (including Hypseloconellacea). Neither the higher systematic position of the superfamily nor its composition are discussed further in the present context, although the 3 genera discussed below are considered correctly placed at this time.

Genus *Latouchella* Cobbold 1921

Type species. – *Latouchella costata* Cobbold 1921

Latouchella holmdalense n. sp.

Figs 7, 8

Derivation of name. – After Gustav Holm Dal and the Holm Dal Formation.

Holotype. – MGUH 18.678 from GGU collection 225535 (Fig. 7A, B, H), Holm Dal Formation.

Material. – Almost 20 specimens from GGU collections 225529, 225535, 225537, 225561, 225563 and 271414; half these specimens are from GGU 225535 (Figs 2–4).

Description. – Laterally compressed species of *Latouchella* with less than one whorl; the apex strongly curved and overhanging the concave sub-apical surface. Rate of expansion relatively high such that height is about three quarters of length (left to right in Fig. 7A, D). Aperture convex in lateral view, flattened near the abapical margin but increasing in curvature toward the adapical margin with passage into a prominent sub-apical fold. Dorsal surface with prominent convex plications separated by narrower concave depressions. The plications vary in expression between individuals (compare Fig. 7A, D, E) and die out on the lateral areas as the sub-apical surface is approached. Ornamentation of growth lines crossed by finer spiral striations. Shell seemingly relatively thick.

Discussion. – The prominent fold in the sub-apical margin of *Latouchella holmdalense* (Fig. 7A, B) can be compared to similar structures developed in other helcionellaceans, e.g. *Mellopegma* and *Eotebenna,* two genera described by Runnegar & Jell (1976) from the Middle Cambrian of Australia, and *Oelandia* Westergård 1936, as redescribed by Peel & Yochelson (1987).

In *Latouchella penecyrano* Runnegar & Jell 1976 the fold is equally well developed as in *L. holmdalense,* although this Middle Cambrian species from Australia has strongly developed spiral lirae and only subdued transverse plication. *Latouchella terraustralis* (Runnegar & Jell 1976), also from the Middle Cambrian of Australia has more widely expanded apertural margins than known material of *L. holmdalense* (but this partly reflects ontogenetic differences since shells become relatively wider with increased growth) and a less pronounced sub-apical fold. The Australian species is distinguished by the narrowness of its more strongly delimited plications relative to the intervening concave areas.

Robison (1964, pl. 92: 11–17) illustrated a suite of specimens from the Wheeler Shale and Marjum Formation of western Utah which he asigned to *"Helcionella" arguta* Resser, 1939. The specimens exhibit considerable variation, noted by Robison (1964: 561) and may not constitute a single species. In particular, the specimen illustrated as fig. 14 closely resembles *L. holmdalense* in the degree of coarseness of the rugae and general coiling, but it appears to lack the fold and emargination on the sub-apical surface.

Latouchella holmdalense differs from the type suite of Resser's species in its less coarse ornamentation. The rugae of the latter are broader (measured spirally) and more globose; they are separated by deep and narrow furrows. *Latouchella burlingi* Resser 1939, described from the lower Middle Cambrian of Utah and Idaho, also has broad rugae but these are not so inflated and strongly delimited as in *L. arguta* which is of the same age. All three species combine spiral threads with transverse growth ornamentation, but the resultant reticulation is most conspicuous in *L. arguta.*

Latouchella costata Cobbold 1921, the type species from the Lower Cambrian of Shropshire is less rapidly expanding and has fewer, more prominent plications tha *L. holmdalense.*

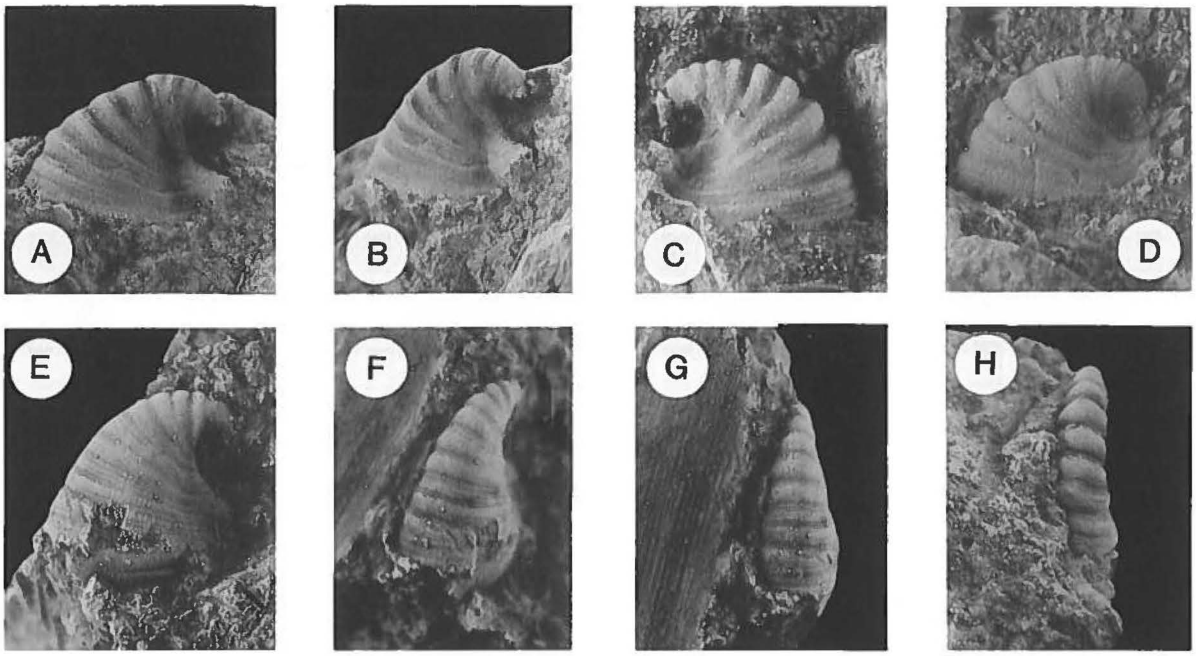

Fig. 7. *Latouchella holmdalense* n. sp.
A, B, H, MGUH 18.678, holotype, in lateral, oblique lateral and abapical views, note the prominent fold on the sub-apical surface. C, MGUH 18.679 in lateral view. D, MGUH 18.680 in lateral view. E-G, MGUH 18.681 in lateral, oblique lateral and abapical views. All specimens from GGU collection 225535, X 10.

Latouchella pearylandica n. sp.

Figs 9–11

Derivation of name. – From Peary Land.

Holotype. – MGUH 18.684 from GGU collection 225561.

Material. – Common in GGU collection 225561, but also present in GGU collections 225529 and 271414 (Figs 3, 4).

Description. – Laterally compressed species of *Latouchella* with more slowly expanding shell than *L. holmdalense* and without the sub-apical fold. In preserved material the height is greater than the length (left to right in Fig. 9A), although this may partly be a function of the growth stage. In lateral view the apertural margin is almost flat, although a very shallow emargination in the lateral area is visible in some specimens (Fig. 9A). Dorsum convex with a tendency to be flattened in some specimens (Fig. 9C). Ornamentation of numerous closely spaced plications of similar width to the intervening troughs; minor secondary plications may be interdigitated between those of the first order in the dorsal area at later growth stages (Fig. 9A).

Discussion. – *Latouchella pearylandica* is easily distinguished from *L. holmdalense* by the fineness of its plication and the taller shell. *L. accordianata* Runnegar & Jell 1976 from the Middle Cambrian of Australia includes forms with similar fineness of plication but individual plications are acute in cross-section, rather than cord-like as in *L. pearylandica*. *L. accordianata* is also less laterally compressed than the Greenland species.

Fig. 8. *Latouchella holmdalense* n. sp. MGUH 18.682 from GGU collection 225561 in lateral and two oblique lateral views, X 20.

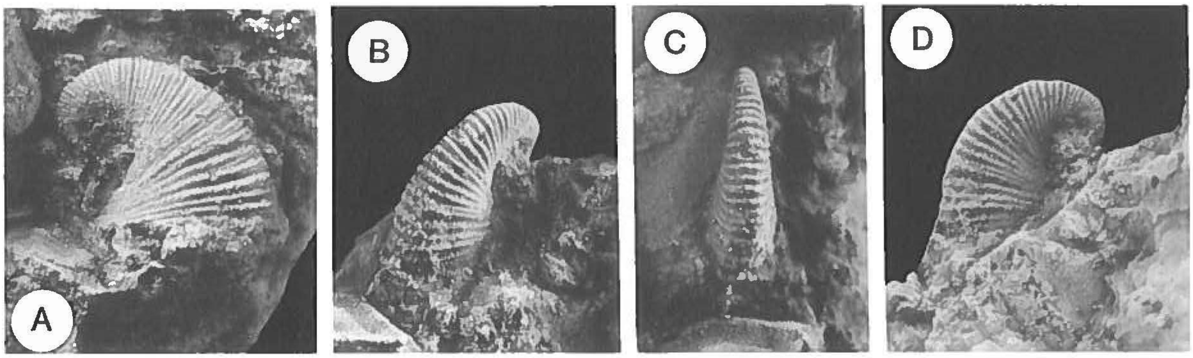

Fig. 9. *Latouchella pearylandica* n. sp.
A, MGUH 18.683, lateral view showing a shallow lateral emargination indicated by slight adapertural concavity in the plications, X 10. B, C, D, MGUH 18.684, holotype, in oblique lateral, dorsal and lateral views, X 13. Both specimens from GGU collection 225561.

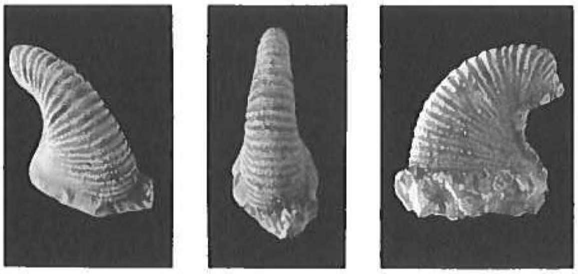

Fig. 10. *Latouchella pearylandica* n. sp.
MGUH 18.685 from GGU collection 225561 in oblique lateral, dorsal and lateral views, X 10.

Latouchella iacobinica Geyer 1986 from the Middle Cambrian of Marocco has a similar high form to *L. pearylandica* but coarser ornament. *L. arguta* Resser 1939 and *L. burlingi* Resser 1939 are both readily distinguished by the coarseness of their comarginal ornamentation.

Genus *Perssuakiella* n. gen.

Type species. – *Perssuakiella troelseni* n. gen. n. sp.

Diagnosis. – Small helcionellacean with just less than one whorl in which the globose, uniformly convex early growth stage is succeeded by a brim-like expanded late growth stage which is elongated in the plane of symmetry of the shell. Shell ornamentation of fine growth lines and revolving fine lirae.

Discussion. – *Perssuakiella* is reminiscent of the early stages of at least some species of *Helcionella* Grabau & Shimer 1909, where a smooth protoconch forming about the first half whorl is abruptly succeeded by the first step-like plication. *Perssuakiella* is distinguished from the early growth stage of such species of *Helcionella* by its greater globosity which clearly gives the impression of a small adult rather than a juvenile. *Perssuakiella* resembles *Protowenella* Runnegar & Jell 1976 in the uniformly convex character of the whorl profile, without prominent plications or rugae. The expanded late growth stage seen in the available specimen of *Perssuakiella* is not known in *Protowenella*, although most material assigned to this latter genus is known from phosphatised internal moulds which lack true apertures. One specimen of *Protowenella* in the type collection from the Middle Cambrian of Australia, shows a constriction on the internal mould reminiscent of the brim (which, however, is not constricted) in *Pers-*

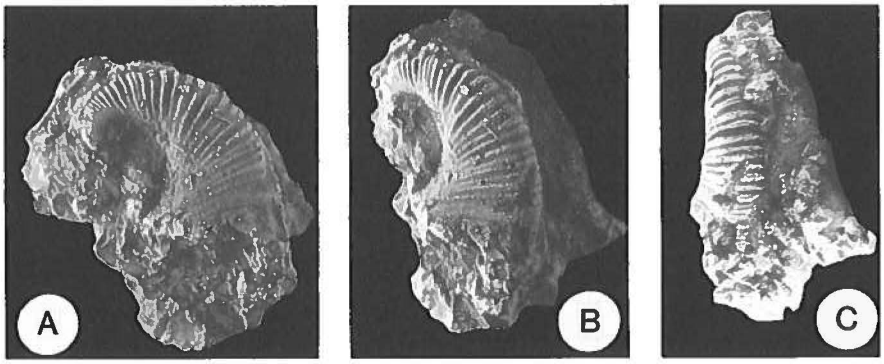

Fig. 11. *Latouchella pearylandica* n. sp.
A-C, MGUH 18.686 from GGU collection 225561 in lateral, oblique lateral and dorsal views, note the tendency for plications on the dorsum to divide (B, C), X 9.

suakiella. Conspicuous folds on the internal mould in the umbilical region are also present in *Protowenella* (Runnegar & Jell 1976; Berg-Madsen & Peel 1978). There is no evidence of their presence in *Perssuakiella* as known but they may not be visible on the shell

Protowenella was originally interpreted by Runnegar & Jell (1976) as a monoplacophoran, assigned to the Family Multifariidae Bjaly 1973 of the Superfamily Bellerophontacea M'Coy 1851. Berg-Madsen & Peel (1978), in describing a specimen from the Middle Cambrian of Bornholm, restored *Protowenella* as a monoplacophoran on the basis of possible reconstruction of water circulation patterns within the mantle cavity. They noted that the configuration of water currents was quite distinct from that suggested for bellerophontaceans such as *Knightites* Moore 1941 and *Plectonotus* Clarke 1899 and thus rejected the suggestion that the Bellerophontacea was a superfamily within the Monoplacophora. Placement of *Protowenella* within the Multifariidae was tentatively accepted, but this family was excluded from the Bellerophontacea.

While clearly helcionellid, *Perssuakiella* partly bridges the morphological gap between this family and *Protowenella*, suggesting that the latter may also be a member of the Helcionellacea. Some material identified as *Protowenella* in the literature possibly represents early growth stages of *Helcionella* or related genera.

The reconstruction of the mantle cavity in *Protowenella* suggested by Berg-Madsen & Peel (1978) requires some modification to accord with this helcionellacean model (see discussion of *Yochelcionella* by Geyer 1986 and of *Oelandia* by Peel & Yochelson 1987). The umbilico-lateral spiral folds in *Protowenella* are still interpreted as marking the location of the inhalant currents to the mantle cavity but the exhalant current is now expected to have emerged below the coiled earlier portion of the shell (sub-apical margin) instead of at the dorsal (abapical) margin.

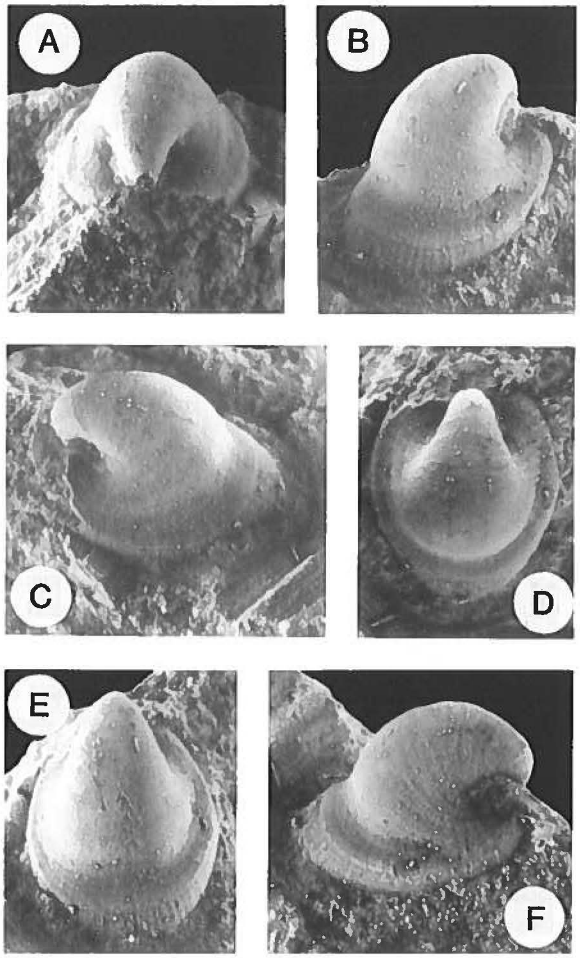

Fig. 12. *Perssuakiella troelseni* n. sp.
A-F, MGUH 18.687 from GGU collection 225537, holotype, X 15. A, oblique adapico-dorsal view; B, C, F, oblique lateral views, note the concave upper surface to the marginal brim, falsely giving the impression of a constriction, and the prominent growth line at the adapical margin of the outer surface of the brim; D, dorsal view, note the upper surface of the brim; E, oblique dorsal view.

Perssuakiella troelseni n. gen. n. sp.

Fig. 12

Material. – MGUH 18.687 from GGU collection 225537, holotype and only known specimen (Fig. 2).

Derivation of name. – For Johannes C. Troelsen, in recognition of his contribution to the study of Lower Palaeozoic geology in North Greenland.

Description. – Small helcionellacean, the type and only known species of *Perssuakiella*, with just less than one full whorl. Umbilici narrow; apex unknown. Early growth stage with globose, uniformly convex dorsum, lacking rugae or plications; passing abruptly into a more widely expanded, brim-like, final growth stage. The initial expansion of the shell in this brim produces a concave surface which delimits the upper (adapical) surface of the brim (Fig. 12F). A prominent growth line marks the adapertural margin of the concave surface, after which there is an angular junction with the outer surface of the brim. This outer surface expands more rapidly than the initial, globose, growth stage, but less rapidly than the first increase in shell expansion producing the upper surface of the brim. Aperture tangential; initially elongate but becoming equidimensional just prior to the brim. In the final preserved growth stage the aperture is elongate and about one fifth longer than the shell width in plan view (Fig. 12D).

Dorsum with suggestion of a shallow median sinus in early growth stages; apertural margin slightly convex in lateral view in the final preserved growth stage, such that shallow emarginations are present in both the dorsal and sub-apical margins.

Ornamentation of growth lines crossed by fine spiral lirae; the latter most prominent on the outer surface of the brim.

Discussion. – The only known specimen is well preserved in limestone, and clearly shows the fine reticulate ornamentation. For comparison, see discussion of genus, above.

Genus *Scenella* Billings 1872

Type species. – *Scenella reticulata* Billings 1872

Discussion. – Yochelson & Gil Cid (1984; see also Stanley 1986) transferred *Scenella* from the Phylum Mollusca to the Suborder Chondrophorina of the Phylum Coelenterata (Class Hydrozoa), mainly on the basis of their description of a new species *(S. morenensis)* from the Lower Cambrian of Spain. This species was subsequently transferred to a new genus, *Marocella,* of uncertain systematic position by Geyer (1986: 96), while *Scenella* was maintained as a mollusc (Geyer 1986: 90–91; see also Berg-Madsen & Peel 1986).

As with many Cambrian molluscs, the systematic position of *Scenella* is the subject of debate in the literature. Apart from interpretation as a chondrophorine (Yochelson & Gil Cid 1984), *Scenella* has been interpreted as a gastropod (historical placement revived by Harper & Rollins 1982; see also Starobogatov 1970), a helcionellacean monoplacophoran (Runnegar & Jell 1976) and a possible tryblidiidan monoplacophoran (Geyer 1986). The relationship to *Helcionella* Grabau & Shimer 1909 expressed by Runnegar & Jell (1976: 116) currently seems most acceptable. As noted by Yochelson & Gil Cid (1984), material with muscle scars assigned to *Scenella* by Rasetti (1954: see also Knight & Yochelson 1960) is best excluded from the genus.

Scenella sp.

Fig. 13

Material. – MGUH 18.688 from GGU collection 225530, Holm Dal Formation (Fig. 3).

Description. – A single well preserved specimen, lacking the apex, is placed here. The shell is oval in plan view (Fig. 13B) with a length:width ratio of 5:4; original height was probably a little more than half the length. The apex was located eccentrically to produce a subapical surface (right in Fig. 13C) which was shorter and more steeply inclined than the dorsal surface (left in Fig. 13C). All surfaces slope away from the apex with convex curvature. Shell ornamentation consists of a fine and even reticulation of radial and concentric elements.

Discussion. – This is a higher shell, lacking the conspicuous overhanging apex of *Marocella* Geyer 1986. In addition, all surfaces are convex in the Holm Dal speci-

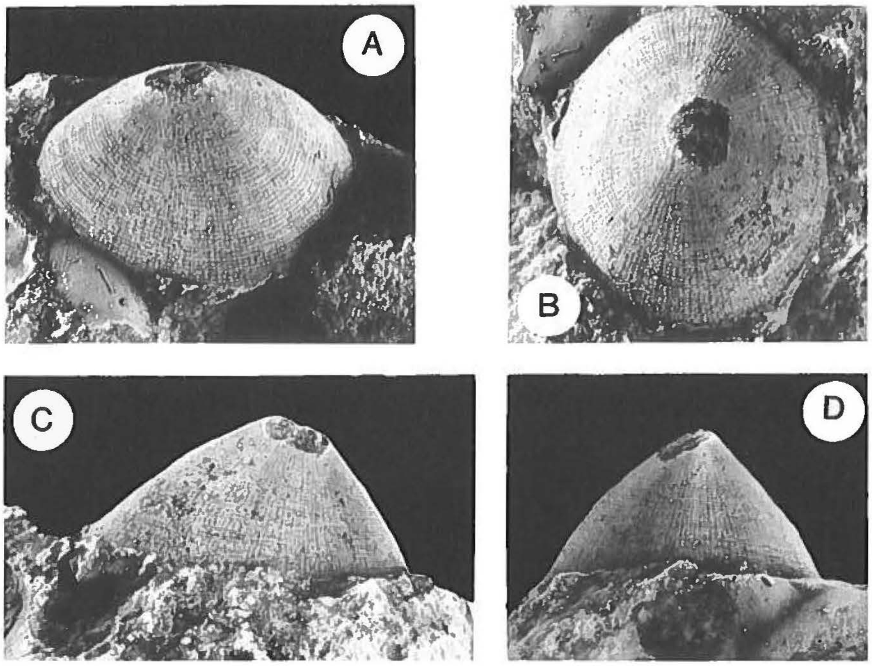

Fig. 13. *Scenella* sp. MGUH 18.688 from GGU collection 225530, X 8. A, oblique dorso-lateral view; B, plan view showing the eccentric (broken) apex located nearer to the top of the illustration; C, lateral view; D, profile when viewed from the sub-apical margin.

men (Fig. 13C, D). *Scenella barrandei* (Linnarsson 1879) from the Middle Cambrian of Baltoscandia is also distinguished by its more eccentric apex and less strongly convex surfaces.

Scenella sp. compares closely with the paratype of the type species from the Lower Cambrian of Conception Bay, Newfoundland, figured by Knight (1941, pl. 2: 5c). This is a smaller specimen than the lectotype in which the convex curvature of all shell surfaces is replaced near the aperture by concave curvature as the shell expands. Periodic coarser concentric ornamentation serves to distinguish *S. reticulata* from *Scenella* sp., where growth ornamentation is uniformly developed.

Hypseloconellacea

Tall monoplacophorans from Upper Cambrian and Lower Ordovician strata in North America have traditionally been referred to the genus *Hypseloconus* Berkey 1898. Assigned species show a variety of forms but one face is typically concave and the other convex when the coiled shell is viewed in lateral aspect (Fig. 14B). In other species groups all surfaces of the shell sloping away from the apex are flat; lateral compression is common, such that the aperture is often elongate, oval or narrowing at one end.

In more recent years several additional taxa have been differentiated, among which the Antarctic *Knightoconus* Yochelson et al. 1973 is conspicuous on account of its proposed relevance to the question of the origin of the Cephalopoda (Yochelson et al. 1973). The genus *Shelbyoceras* Ulrich et al. 1943, originally described as a cephalopod, has also been re-interpreted as an unusually tall monoplacophoran related to *Hypseloconus* (Stinchcomb & Echols 1966, Stinchcomb, 1980). Recently, Stinchcomb (1986) introduced six new genera – *Cambrioconus, Orthoconus, Cornuella, Protoconus, Archeoconus* and *Gasconadeoconus* – which he placed within the new Superfamily Hypseloconellacea. His study indicates the presence of a much greater diversity of taxa within this previously neglected and poorly understood group.

During the same general period, Soviet palaeontologists have also described a number of new monoplacophoran taxa; these have included several relatively tall shells, although comparisons with *Hypseloconus* have generally not been made. An exception is the study by Rozov (1975) where a new Order Kirengellida contained a new Family Romaniellidae containing both *Hypseloconus* and its stated synonym *Romaniella* Doguzhaeva 1972. Since the only other taxon placed within the family is the new genus *Nyuella* there seems little justification for accepting Romaniellidae in preference to the Hypseloconidae Knight 1956, even though the stated synomymy of *Romaniella* and *Hypseloconus* is not accepted here.

Common to many of these Upper Cambrian to Lower Ordovician monoplacophoran taxa is difficulty in restoration and interpretation of the living animal. Muscle scars are known in most recently described taxa. However, interpretation of the significance of the patterns is speculative and frequently is based upon comparison with geologically younger taxa (such as *Pilina* Koken 1925 and *Tryblidium* Lindström 1880) which need not be close phylogenetic relatives. The question of recognising anterior *contra* posterior is fraught with problems and there exists great uncertainty as to whether or not the apex in the generally slightly coiled, cap-shaped shells always lies anteriorly (as in the Recent *Neopilina*), if it may be posterior in some groups or if its position has no greater meaning within the phylogeny of the monoplacophorans. The direction of coiling of the shell also needs to be considered. Coiling may be exogastric, i.e. with the earlier coiled portion anterior (as is the case in *Pilina* and *Tryblidium*), or endogastric with the earlier coiled portion lying posterior (as in gastropods). However, differential growth of the apertural margins can place the apex anterior or posterior irrespective of the direction of coiling.

An example of the difficulties associated with restoration is provided by the genus *Kiringella* which Rozov (1968) proposed for cap-shaped shells of medium size from the Upper Cambrian of Siberia in which the apex was located slightly eccentrically. He described six pairs of muscle scars forming a U-shape in plan view, of which two pairs forming the prongs of the U-shape were fused into a large composite pair judged to lie posterior to the apex. Thus the apex was interpreted by Rozov (1968) as lying nearer to the anterior margin of the shell in *Kiringella* as is also the case with *Pilina* and *Tryblidium*. Yochelson et al. (1973) rejected this interpretation of *Kiringella*. By comparison with the same *Pilina* and *Tryblidium* (Lindström 1884, Lemche & Wingstrand 1959, Peel 1977, Wingstrand 1985), Yochelson et al interpreted the large composite pair of muscle scars in *Kiringella* as anterior. Hence, the apex was considered to be displaced toward the posterior and the shell reoriented 180 degrees with respect to the interpreted orientation of Rozov (1968). Stinchcomb (1980) arrived at the same conclusion as Yochelson et al. (1973) following a slightly different line. He noted that the open end of the U-shape of muscle scars lies anterior in *Pilina* which would also suggest that the apex in *Kiringella* was posterior and not anterior as was originally suggested by Rozov (1968).

Muscle scars in *Hypseloconus* have been described by Stinchcomb (1980) who noted a U-shaped band of 6 pairs of discrete scars when the shell is viewed in plan view which he interpreted as opening anteriorly (as in *Pilina*). The typical shell form in *Hypseloconus* is thus apparently endogastric, although in lateral view the apex is located near the anterior. The anterior surface is convex and the posterior surface is concave. This shell form is unusual among monoplacophoran molluscs and suggests a coiling direction opposite to the exogastric coiling seen in *Pilina* and *Tryblidium*. Therefore, a natural speculation might be that the tryblidiacean and the hypseloconellacean stocks are not closely related. While both are reasonably interpreted as untorted molluscs (monoplacophoran in a loose sense) such an apparently fundamental difference in shell form is otherwise difficult to reconcile.

The dilemma can be resolved, however, by comparison with another untorted mollusc, the helcionellacean *Yochelcionella ostentata* Runnegar & Jell 1976 from the Middle Cambrian of Australia (Runnegar & Jell 1976: fig. 11C. Shell form in *Y. ostentata* is very reminiscent of that in *Hypseloconus*, with well developed concave and convex surfaces in lateral aspect (the latter carries the tubular snorkel characteristic of *Yochelcionella*). Indeed, Pojeta & Runnegar (1976) interpreted the convex side as anterior (as in *Hypseloconus*) based on a reconstruction of mantle cavity structure (see Runnegar & Pojeta 1985 for a full review), although Geyer (1986) and Peel & Yochelson (1987) preferred to reconstruct the convex surface as posterior on the basis of an alternative mantle cavity reconstruction. This difference from *Hypseloconus* is not important in the present context, however, since *Yochelcionella* as an helcionellacean is only distantly related to the tryblidiaceans and hypseloconellaceans. Of relevance, however, is the ontogenetic form of *Yochelcionella ostentata* (Runnegar & Jell 1976: fig. 11C) which clearly demonstrates that the tall shell undergoes a change in coiling direction during growth. Adopting the orientation of Geyer (1986) and Peel & Yochelson (1987), with the snorkel located posteriorly, it can be seen that the initial part of the shell is coiled endogastrically as in other helcionellaceans. After formation of the snorkel, coiling gradually changes to exogastric with the development of the prominent anterior concave surface characteristic of the adult of the species but atypical of helcionellaceans in general.

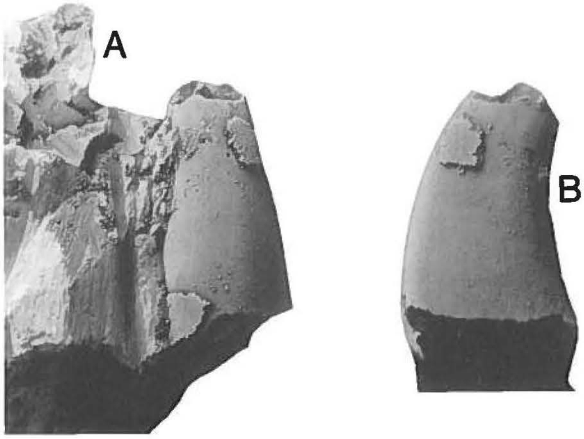

Fig. 14. *Hypseloconus* sp.
MGUH 18.689 from GGU collection 225529, X 5. A, profile viewed from the abapical margin, i.e. left in B; B, lateral view, note the convex and concave surfaces characteristic of Hypseloconus.

The apparently anomalous coiling of *Hypseloconus* can be resolved with that of the tryblidiaceans by invoking similar allometric growth to that clearly demonstrated in *Y. ostentata*, an interpretation which allows similar orientation of muscle fields in *Hypseloconus* and, for example, *Pilina*.

Early growth stages are not known in most tall hypseloconellaceans. An exception is provided by Antarctic *Knightoconus* figured by Webers et al. (in press) in which the endogastrically coiled apex overhangs the convex surface (in lateral view) of the exogastrically coiled adult.

Family Hypseloconidae Knight 1956

Genus *Hypseloconus* Berkey 1898

Type species. – *Hypseloconus recurvus* Berkey 1898

Hypseloconus sp.

Figs 8, 14

Material. – MGUH 18.689 from GGU collection 225529 and MGUH 18.690 from GGU collection 225537, Holm Dal Formation (Figs 2, 3). A poor specimen, possibly *Hypseloconus* sp., is present in GGU collection 225563.

Discussion. – Two poorly preserved fragments are figured here. The smallest is an internal mould of the early stages of a very tall hypseloconellacean species with a slightly elongate aperture, angulated below the convex surface (left in Fig. 14B). The apex and aperture are broken.

The largest specimen (Fig. 15) preserves much of the latest growth stage but intermediate and early stages are broken away. The shell was also a tall slowly expanding cone, apparently elongate in cross-section at the earliest preserved stage although the preserved aperture is equidimensional. The apertural margin below the convex surface is not preserved but Stinchcomb (1980, 1986) has noted that the aperture commonly narrows in this direction which he interpreted as anterior. Adherent patches of shell retain fine growth lines.

There is no morphological or ontogenetic overlap between the two specimens, although both indicate tall, relatively slowly expanding hypseloconellacean species.

Hypseloconus bonneterrense Stinchcomb 1975 from the Dresbachian Bonneterre Formation of Missouri is

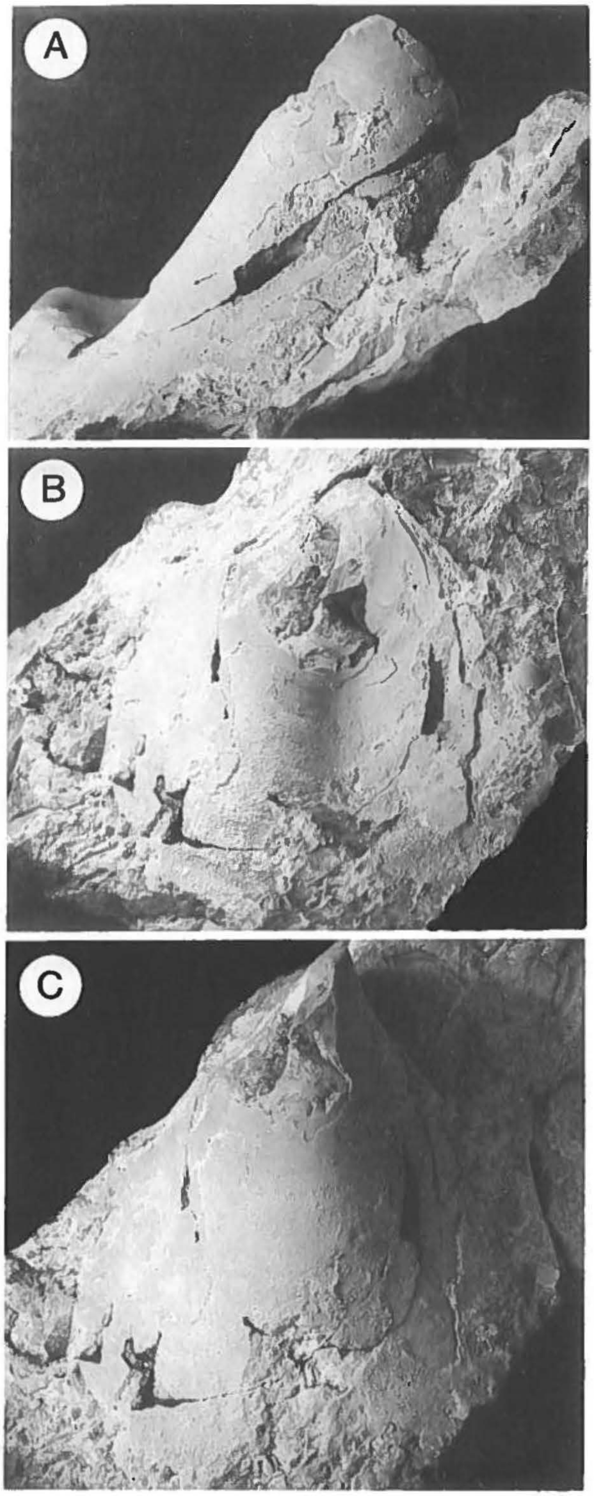

Fig. 15. *Hypseloconus* sp.
MGUH 18.690 from GGU collection 225537, only aperture preserved, X 4. A, lateral view showing the pronounced concave surface (left) interpreted as posterior; B, apical view showing the equidimensional plan of the aperture as preserved; C, oblique view of expanded aperture.

similar in form to the Greenland material, although the specimen in Fig. 14 appears to be even more slowly expanding. The larger Greenland specimen has a more flaired aperture; this could be an ontogenetic effect since the Missouri specimens are somewhat smaller.

Cornuella parva Stinchcomb 1986 from the Upper Cambrian Eminence Formation of Missouri is distinguished by its small size, greater curvature of the very tall shell and more cord-like growth ornament. *Orthoconus striatus* Stinchcomb 1986, also from the Eminence Formation, lacks the apertural flare of the Greenland material and has prominent spiral ornamentation. *Knightoconus* Yochelson et al. 1973 from the Upper Cambrian of the Antarctic has a similar tall shell but early stages seem to be more circular in cross-section than the smallest of the two Greenland specimens (Fig. 8). The internal septa considered by Yochelson et al. to be characteristic of *Knightoconus* have not been observed in available specimens from the Holm Dal Formation. *Shelbyoceras* Ulrich et al. 1943 has a tall septate shell with longitudinal striations, apparently lacking the flared aperture of the Holm Dal material (Stinchcomb 1980).

Hypseloconellacean sp.

Fig. 16

Material. – MGUH 18.691 from GGU 225537, from the type locality of the Holm Dal Formation (Fig. 2).

Description. – The single specimen placed here is a mainly exfoliated internal mould and associated partial external mould; the apertural margin is not preserved. It is a large (length about 20 mm), high, laterally compressed form; height was probably somewhat less than the length of the complete shell (left to right in Fig. 16B) while width (left to right in Fig. 16A, C) is about two-thirds of length. The apex is displaced slightly from the centre, thus lying slightly closer to the margin interpreted as adapical (right in Fig. 16B). Slight apical overhang produces a shallow concavity in the lateral profile of the sub-apical surface just below the apex and corresponding shallow convexity in the dorsal (abapical) surface. In plan view (Fig. 16F) the shell is broadest near the adapical margin, where the apertural margin is uniformly rounded; the aperture narrows abapically where dorso-lateral shallow excavations on the internal mould, running from the apex to the apertural margin (Fig. 16E-G), delimit a dorsal fold (slight lateral crushing on the right side in Fig. 16F possibly emphasises delimitation of the fold).

The shell was apparently ornamented solely with concentric growth lines, traces of which are preserved on the internal mould (Fig. 16D, E, G). Muscle scars are not preserved.

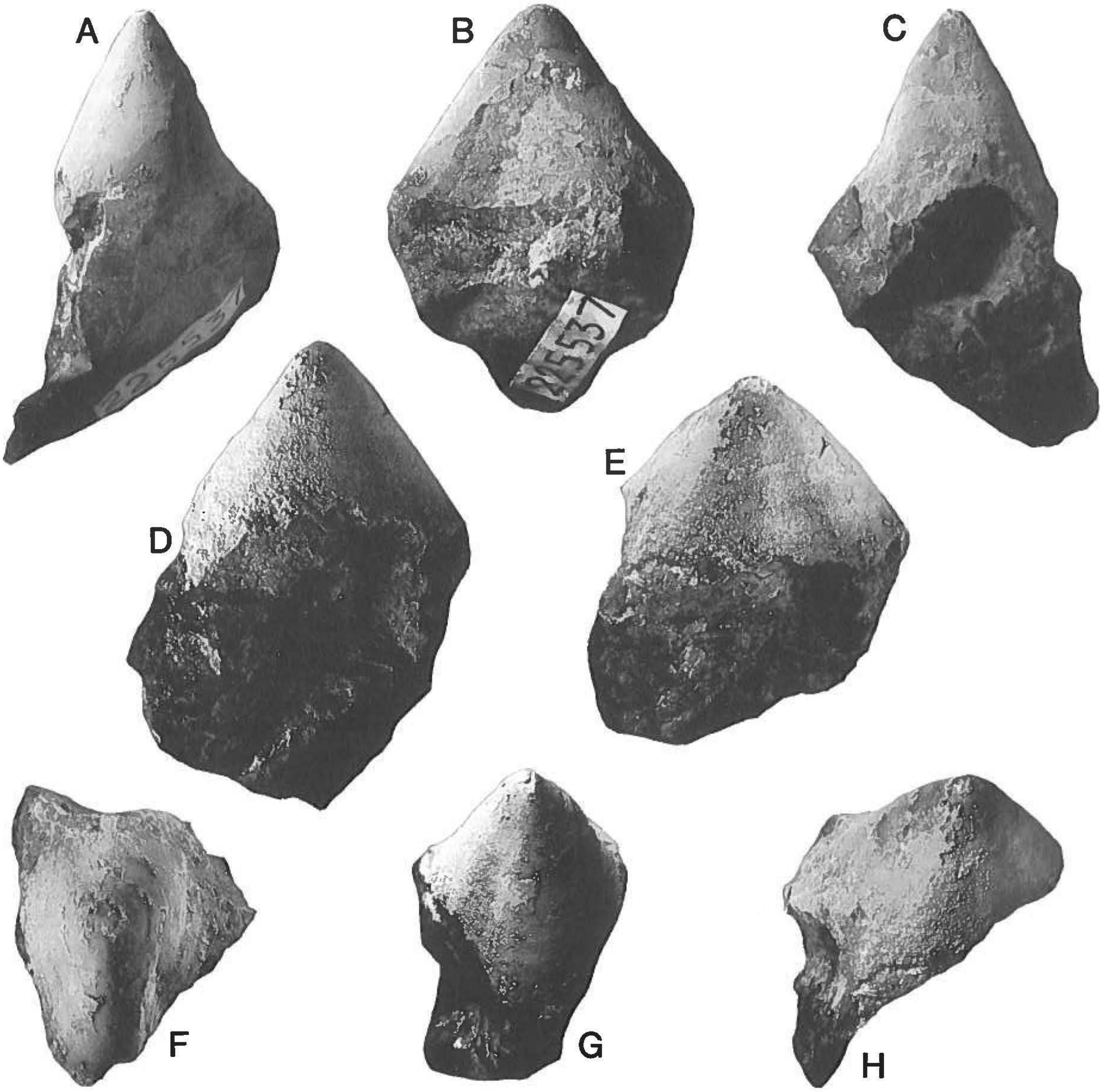

Fig. 16. Hypseloconellacean sp.
MGUH 18.691 from GGU collection 225537, internal mould with traces of partly exfoliated shell, X 2. A, profile viewed from abapical margin i.e. from left in B, note slight crushing of fold (right); B, lateral view with the slightly crushed fold to the left, note slight concave curvature of sub-apical surface (right); C, profile viewed from adapical margin i.e. from right in B; D, lateral view with concave sub-apical surface to left; E, oblique lateral view of same side as D showing fold to right; F, apical (plan) view showing apical fold (bottom) and uniformly convex sub-apical apertural margin; G, as E but with increased dorsal obliquity; H, as E but with increased apical obliquity.

Discussion. – *Kiringella ayaktchica* Rozov 1968, the type species of *Kiringella* Rozov 1968 from the Upper Cambrian Mansiysk horizon of the Siberian platform, is a smaller species with a generally lower shell lacking the dorsal fold. However, illustrations given by Rozov (1968, fig. 3) suggest considerable variation in the form of the cone within limits possibly including the Greenland specimen. *Kiringella kultavasaensis* Doguzhaeva 1972 from the Lower Ordovician of the Urals is similar in height and degree of lateral compression to Hypseloconellacean sp. but the concave sub-apical surface is longer than the convex dorsal surface in the Soviet species.

Yochelsonella compressa Flower 1968 from the Lower Ordovician of New York State is a taller species than Hypseloconellacean sp., with greater lateral compression. The Greenland specimen resembles *Gasconadeoconus waynesvillensis* Stinchcomb 1986 from the Lower

Ordovician of the central United States in the presence of the dorsal fold, but Stinchcomb (1986) considered this genus to be characterised by radial ornamentation. *G. waynesvillensis* was only illustrated from a single aspect (considered anterior by Stinchcomb) to show the fold and the slope of the lateral areas; the latter are shallowly concave near the apex and not slightly convex as in Hypseloconellacean sp. (Fig. 16A). In addition, the apex in *G. waynesvillensis* is stated to lie closer to the margin bearing the fold, whereas the fold in Hypsoconellacean sp. from the Holm Dal Formation lies at the margin farthest from the apex. The Missouri species also tends to be higher than long, whereas the opposite relationship exists in the Greenland specimen.

The question of orientation, discussed above, is not clearly resolved in this hypsoconellacean from the Holm Dal Formation. By comparison with *Gasconadeoconus* and species of *Hypseloconus,* the narrow abapical margin and fold should indicate the anterior margin. The apex, however, lies slightly closer to the opposite (presumed posterior) margin. In the absence of additional material permitting assessment of variation in the position of the apex and details of musculature, the species can not be more precisely assigned.

Kiringella sp.

Fig. 17

Material. – MGUH 18.692 from GGU collection 225561, a single internal mould, Holm Dal Formation (Fig. 3).

Description. – Small cap-shaped shell with eccentric apex, known only from a single internal mould. In plan view the apertural margin is pear-shaped, with greatest width near the adapical margin (bottom in Fig. 17A), narrowing toward the abapical margin. Slope from apex to adapical margin is steeper than that toward the abapical margin (Fig. 17B); these surfaces, and the lateral surfaces are flat (Fig. 17C). Dorsal surface between apex and abapical margin is slightly angulated. Internal mould with poorly delimited structures on both lateral areas (dark shadows on left and right sides in Fig. 17A) which may represent muscle scars, although confirmative detail lacking; form of these possible scars suggests a U-shaped distribution open toward the abapical margin. Shell ornamentation unknown.

Discussion. – If the shadow-structures present on the internal mould are correctly interpreted as muscle scars, the open end of the U-shaped pattern would be interpreted as anterior, with the apex lying nearer to the posterior margin of the shell. This would justify placement in *Kiringella,* following Yochelson et al. (1973), although Webers et al. (in press) employ a more loose interpretation.

Kiringella sp. is a lower shell than *K. ayaktchica* Rozov 1968 from the Upper Cambrian of the Siberian platform and narrows more strongly toward the supposed anterior. It is lower than Hypseloconellacean sp. (Fig. 16) and lacks the pronounced curvature of *Hypseloconus* sp. (Fig. 14).

Kiringella? sp. cf. *K? washingtonense* (Stinchcomb 1975)

Figs 18, 19

Material. – MGUH 18.693 from GGU collection 225537, MGUH 18.694 from GGU collection 225561, Holm Dal Formation (Figs 2, 3).

Description. – A large (length about 20 mm) cap-shaped shell with a sub-central apex and with the height probably somewhat less than the length; width about

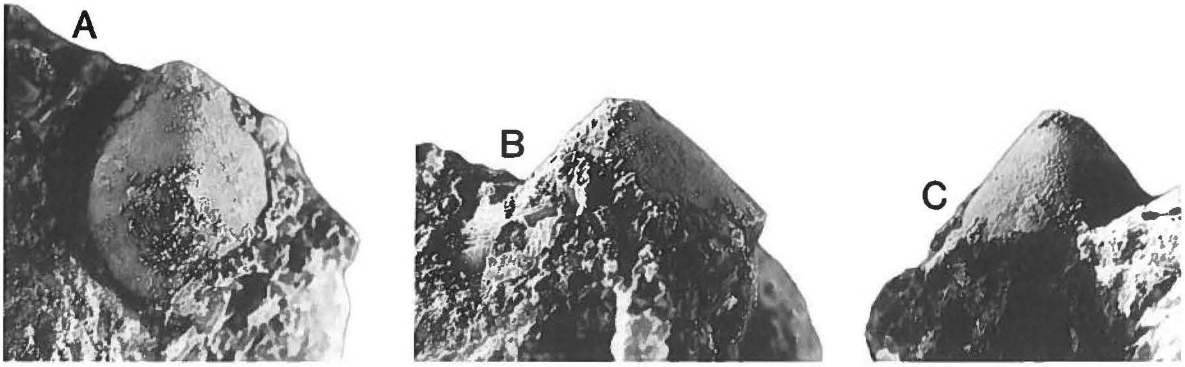

Fig. 17. *Kiringella* sp.
MGUH 18.692 from GGU collection 225561, X 7. A, apical (plan) view showing apex located nearer to the presumed posterior (lower) margin, note shadows of possible muscle scars to left; B, lateral view with apex located nearer to left margin of illustration; C, profile of lateral surfaces viewed from the presumed anterior (top in A).

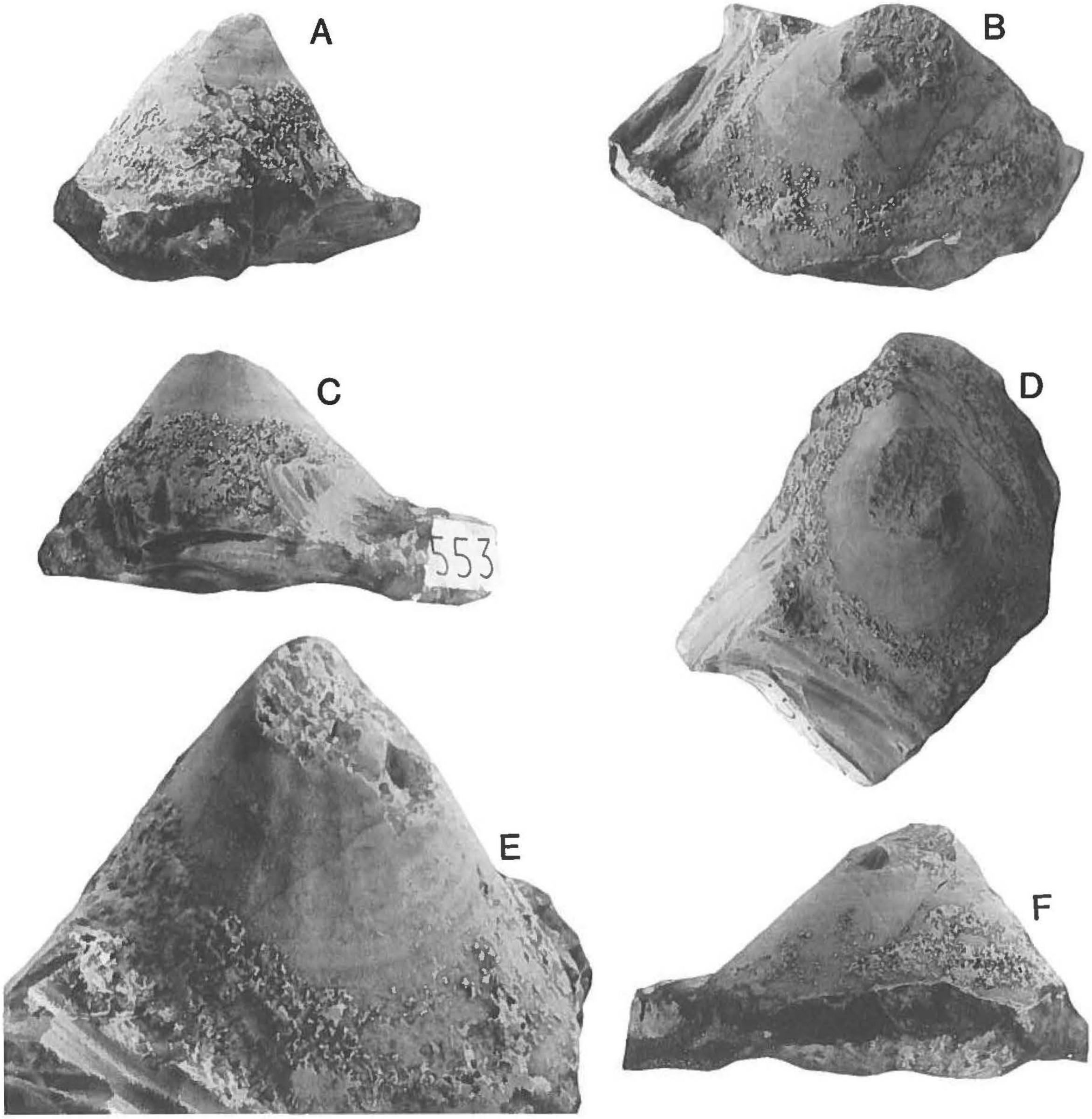

Fig. 18. *Kiringella?* sp. cf. *K? washingtonense* (Stinchcomb 1975)
MGUH 18.693 from GGU collection 225537, internal mould with broken apex, X 2 unless stated. A, profile of lateral surfaces viewed from sub-apical surface; B, oblique lateral view, same side as in F; C, lateral view, note steeper sub-apical surface; D, apical (plan) view with the angulated sub-apical surface at the top of the illustration, note the radial structures on the dorsal surface; E, oblique view of dorsal surface showing flat-topped radial ridges on the internal mould interpreted as possible muscle scars, X 4; F, lateral view with sub-apical surface to right.

three-quarters of length. Nature of earliest growth stages not known. The apex is eccentric and the sub-apical surface is more steeply inclined than the dorsal (abapical) surface (Figs 18F, 19C). The aperture is widest at the adapical margin, where the apertural margin is uniformly convex in plan view; it narrows toward the abapical margin such that the abaxial margin is angular in plan view (Figs 18D, 19A). All preserved surfaces of the shell are essentially flat, sloping away from the apex towards the aperture, but it is likely that slight concavity is developed on the lateral surfaces and on the sub-apical surface near the apex.

Shell ornamentation consists entirely of concentric growth lines (Fig. 19). Occasional coarser elements and traces of the finer growth lines may be discerned on moulds of the shell interior (Figs 18, 19).

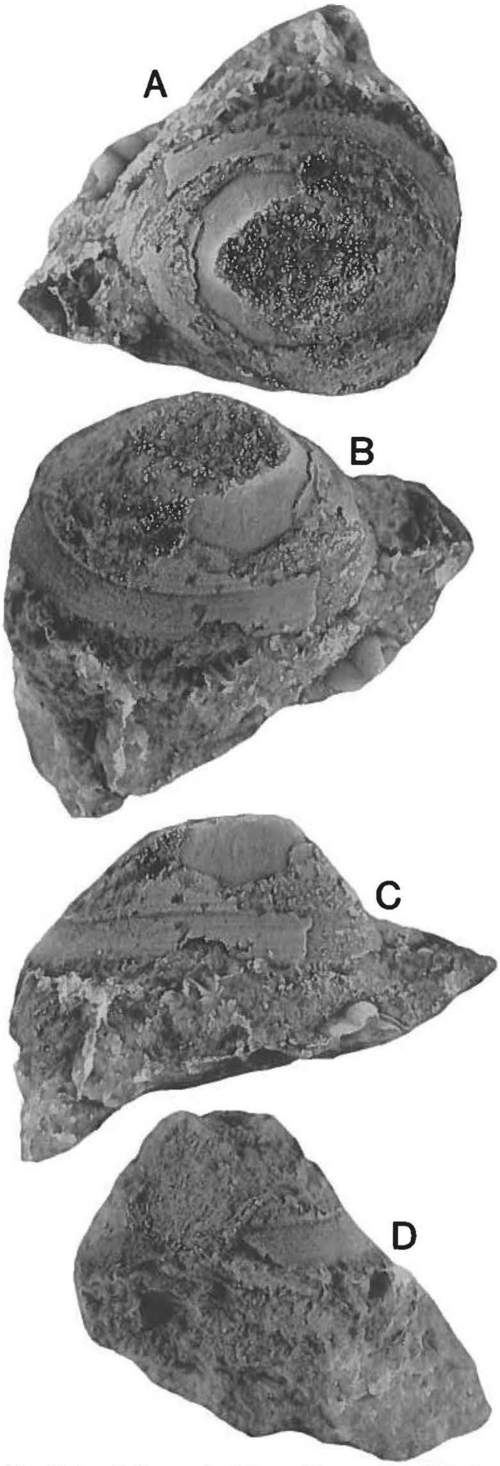

Fig. 19. *Kiringella?* sp. cf. *K? washingtonense* (Stinchcomb 1975)
MGUH 18.694 from GGU collection 225561, partly exfoliated internal mould with broken apex, X 4. A, slightly oblique plan view, note the angulation on the sub-apical surface (left); B, oblique lateral view showing ornamentation; C, lateral view showing the steeper sub-apical surface (right); D, profile showing slope of lateral surfaces, viewed from right in A.

One specimen has radial, flat-topped ridges preserved on the internal mould on its dorsal surface (Fig. 18D, E). Five (possibly 6) ridges are visible; adaperturally they terminate abruptly about half way from the aperture to the apex but their adapical margins are not preserved.

Discussion. – The largest specimen placed here is an internal mould lacking the apex, but preserving impressions of growth ornamentation and the radiating ridges described above (Fig. 18). The angulation extending from the apical region to the apertural margin on the sub-apical surface is conspicuous. The second specimen is smaller but retains much of the shell; it also lacks the apical area but shows the angulation on the sub-apical surface and well developed growth ornamantation near the aperture (Fig. 19).

The radiating ridges on the internal mould (Fig. 18E) are interpreted as muscle scars although it is not possible to ascertain the total complement of muscle scars present or their distribution. In view of the restricted distribution of the 5 or 6 preserved scars it is likely that two or more additional pairs of scars were originally present.

In terms of shape of the shell the Greenland material compares well with Stinchcomb's (1975) species from the Dresbachian Bonneterre Formation of Missouri which was originally referred to *Hypseloconus*. The generic placement of the species is uncertain, due to the lack of reliable information concerning muscle scars. However, the species is much lower spired and lacks the prominent curvature generally associated with *Hypseloconus*. Reference to *Kiringella* is not without problems; the partially preserved elongate muscle scars in the larger Greenland specimen (Fig. 18E) strongly suggest that the angular, sub-apical surface is anterior and the apex thus lies closer to the anterior margin. This is in conflict with *Kiringella ayaktchica* where the elongate muscles lie on the sub-apical surface suggesting that the apex lies nearer to the posterior margin (following the interpretation of Yochelson et al. 1973 which is diametrically opposed to that of Rozov 1968). The issue can not be resolved on the basis of available information; hence even the tentative assignment to *Kiringella* is made without conviction.

Kiringella? sp. cf. *K? washingtonense* differs from *Kiringella* sp. in having its apex located nearer to the presumed anterior margin (Fig. 18D); in the latter, the apex is located nearer to the presumed posterior margin (Fig. 17A).

Paragastropoda

Linsley & Kier (1984) proposed the Class Paragastropoda to accomodate a number of anisostrophically coiled, non-torted molluscs, many of which (Superfamilies Onychochilacea, Macluritacea, ?Euomphalacea grouped in a new Order Hyperstrophina) traditionally have been considered to be gastropods (Knight et al. 1960). A second new order, Orthostrophina, contained the single Superfamily Pelagiellacea Knight 1956, species of which may be numerically conspicuous in Cambrian faunas.

Historically, pelagiellaceans have often been referred to the gastropods, largely on account of their anisostrophically coiled shells. Knight et al. (1960) excluded *Pelagiella* from the Gastropoda but Runnegar and Jell (1976) recognised the superfamily within the archaeogastropod Prosobranchia.

Superfamily Pelagiellacea Knight 1956
Family Pelagiellidae Knight 1956

Genus *Costipelagiella* Horny 1964

Type species. – *Costipelagiella zazvorkai* Horny 1964

Costipelagiella kochi n. sp.

Fig. 20

Derivation of name. – For Lauge Koch, explorer, cartographer, geologist, whose studies and collections in the early part of this century established the framework for North Greenland geology and palaeontology.

Material. – MGUH 18.695 from GGU collection 225561, holotype and only known specimen, Holm Dal Formation (Fig. 3).

Description. – A small; dextrally coiled, almost planispiral shell with about one and a third whorls. Whorl overlap is slight such that sutural indentation is deep. Protoconch globose, smooth, with abruptly rounded adapical termination. The cross-section of the whorl is imperfectly known in detail; in standard orientation with the axis of coiling placed vertically the whorl profile is clearly wider than high (compare Fig. 20C, D). The upper whorl profile is shallowly convex, such that the apex is not visible in lateral view (Fig. 20D). The outer whorl surface is uniformly rounded, without angulation; the basal surface is not known. Ornamentation of growth lines which become costate around the outer whorl face during the last half whorl. Ornamentation delimits a broad, shallow sinus in the outer lip (Fig. 20B, C).

Discussion. – The costate growth lines suggest that this species be placed in *Costipelagiella* Horny 1964, described from the Middle Cambrian of Czechoslovakia, although this form differs in terms of whorl profile from *Costipelagiella kochi*. The type species, *C. zazvorkai* Horny 1964, was also described from a single specimen which differs from the Holm Dal specimen by virtue of its less rounded whorl profile and slightly elevated spire. The upper whorl surface in *C. zazvorkai* is flattened, passing relatively abruptly onto the outer whorl face which slopes in toward the base. The outer whorl face in *C. zazvorkai* appears concave near the aperture (cf. Horny 1964, pl. 2: 2, 3). In these characters the type species is readily distingusihed from *C. kochi* which has convex upper and outer whorl surfaces. In addition, the peripheral sinus of *C. zazvorkai* is deeper than in *C. kochi* and its adapical margin on the upper whorl surface is more abruptly defined.

Costipelagiella kochi is readily distinguished from many species of *Pelagiella* by its rounded whorl profile. The upper whorl surface in *Pelagiella* is commonly strongly flattened and there is rapid transition around a peripheral angulation onto a globose basal surface (cf. *Pelagiella deltoides* Runnegar & Jell 1976 and *P.* sp. cf. *P. lorenzi* Kobayashi 1939 of Geyer 1986).

Robison (1964) described internal moulds referred to *Pelagiella* from the Marjum Formation (late Middle Cambrian) of Utah which show a similar, rounded, whorl profile to *C. kochi*. The rate of expansion in the Marjum Formation species is lower, however, and the spire is slightly elevated.

Pelagiella corinthiana Runnegar & Jell 1976 from the Currant Bush Limestone (Middle Cambrian) of Austra-

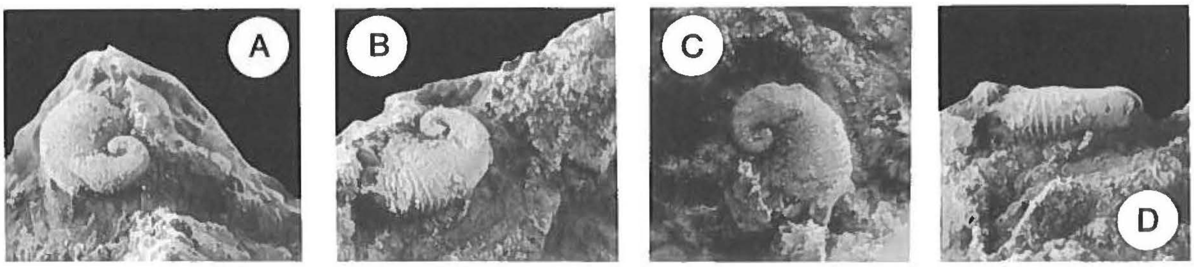

Fig. 20. *Costipelagiella kochi* n. sp.
MGUH 18.695 from GGU collection 225561, X 20. A, B, oblique apico-lateral views; C, apical view; D, lateral view.

lia has a similar whorl profile to *C. kochi* but appears to be more rapidly expanding; details of ornamentation were not given by Runnegar & Jell (1976).

Lochman (1940) gave the name *Pelagiella bridgei* to a similarly rounded species from the Bonneterre Formation of Missouri but her illustrations seem to indicate a sinistral shell with slightly raised spire.

Open coiled euomphalacean (?)

Fig. 21

Figured material. – MGUH 18.696 from GGU collection 225561 (Fig. 3).

Discussion. – This single specimen is so poorly preserved that identification even as a mollusc is tenuous. However, the gentle curvature and presence of longitudinal angulations invite comparison with open-coiled members of the Superfamily Euomphalacea de Koninck 1881. Possible traces of transverse growth lines are present. There is some resemblance to the Devonian genus *Odontomaria* Roemer 1876 but similar open coiled forms have been described recently from the Upper Cambrian by Yochelson (1987) and Yochelson & Stinchcomb (1987). Of these, *Spirodentalium* Walcott 1890 has a whorl profile with grooves (Yochelson 1987: fig. 1.3), while the Greenland specimen has angulations. *Macluritella?* walcotti (Howell 1946) of Yochelson & Stinchcomb (1987: fig. 1) has a pronounced triangular cross-section to the whorl not seen in the specimen from Holm Dal.

Hyolitha

Opinions differ as to the relationships of the Hyolitha and consequently as to its systematic status. Runnegar et al. (1975) suggested similarities betweens hyoliths and sipunculoid worms, but preferred to separate the former as a new phylum. Marek & Yochelson (1976) presented arguments for considering the Hyolitha to be a class within the phylum Mollusca. Sysoyev (1984) rejected these models and proposed a new phylum Hyolithozoes with affinities to bryozoans, brachiopods and phoronids. Discussion of the issue lies outside the present context, although the established term Hyolitha is retained for the systematic unit.

Most authors recognise two major subdivisions within the Hyolitha, the orders Orthothecida and Hyolithida. Sysoyev (1984: 8) divided his phylum into two classes, Orthothecimorpha and Hyolithomorpha. Peel & Yochelson (1984) subsequently assigned the Order Toxeumorphorida of Shimansky (1962) to the Hyolitha, to include some unusually large Carboniferous-Permian hyoliths.

Order Orthothecida Marek 1966

Orthothecid sp.

Fig. 22

Figured material. – MGUH 18.697 and 18.698 from GGU collection 271414 (Fig. 4).

Fig. 21. Open coiled euomphalacean (?)
MGUH 18.696 from GGU collection 225561, X 4. A, note spiral twisting and angulations; B, note traces of possible transverse growth lines at left.

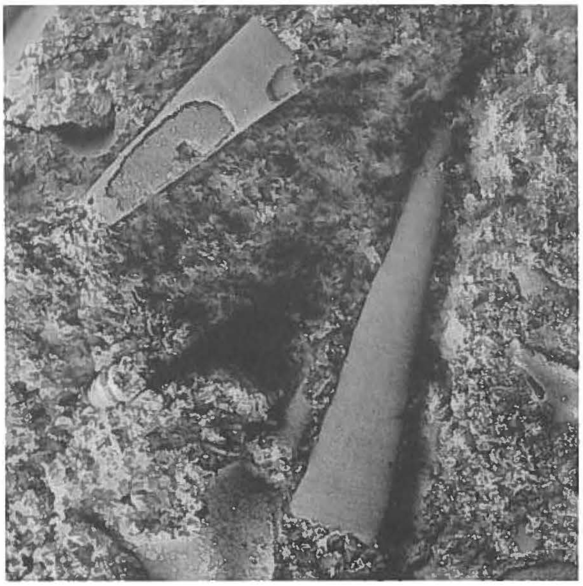

Fig. 22. Orthothecid sp. MGUH 18.697 (left) and MGUH 18.698 from GGU collection 271414, X 8. Note the fine growth lines on the ventral surface of both specimens.

Discussion. – Both of the available small specimens show the ventral surface which is shallowly convex; transverse growth lines indicate a simple orthotheciform aperture without ligua. The dorsal surface is not seen but is clearly more convex than the ventral. No apical to apertural curvature is discernible along the exposed length of both conchs which expand uniformly at 10 degrees. It is not known if the conchs are internally septate.

The flattened ventral surface and inflated dorsum suggest comparison with the families Allathecidae Missarzhevskii 1969 and Chelsonellidae Malinky 1987 but lack of information concerning the dorsal surface prevents closer determination.

Order Hyolithida Sysoyev 1957

Hyolithid sp.

Figs 23, 24

Figured specimens. – MGUH 18.699 from GGU collection 225561, MGUH 18.700 from GGU sample 225530 (Fig. 3).

Discussion. – One fragmentary specimen (Fig. 23) lacks the apex and has the dorsal surface buried in sediment. The exposed ventral surface is shallowly convex with growth lines and weak comarginal rugae indicating a short ligua. In transverse cross-section, the height of the conch is seen to be about half of its width and the dorsum is uniformly convex. A poorly preserved specimen from GGU collection 225529, exposed in lateral aspect but without apex or aperture, may belong here.

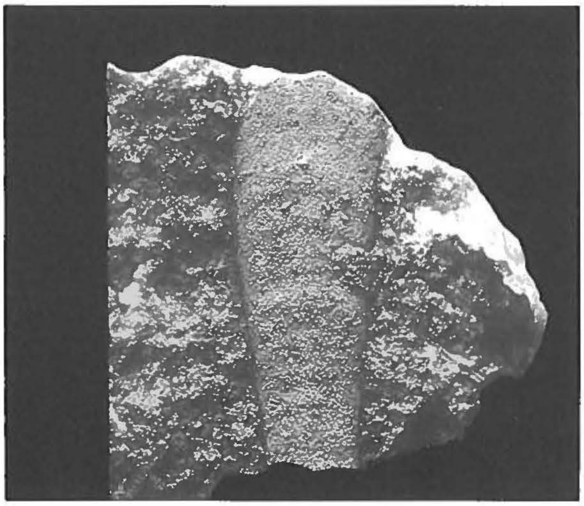

Fig. 23. Hyolithid sp.
MGUH 18.699 from GGU collection 225561, ventral surface note short ligua, X 8.

The second illustrated specimen preserves the dorsal surface, although the aperture and apex are broken (Fig. 24). The conch is more rapidly expanding than the specimen in Fig. 23 and ornamentation consists of fine cords separated by smooth areas of shell.

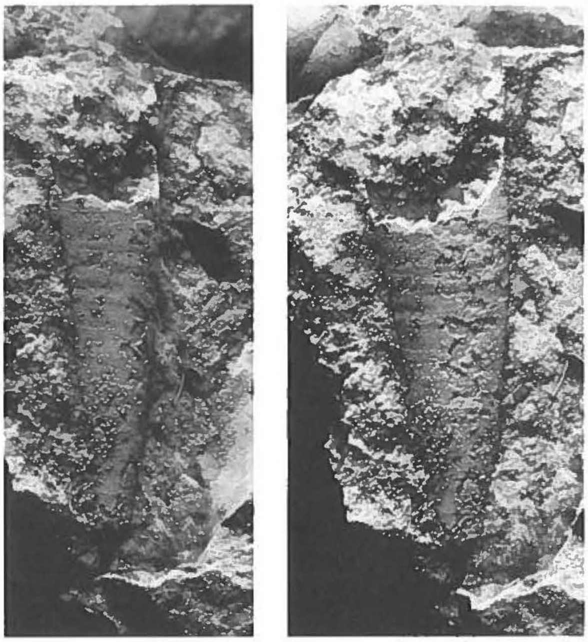

Fig. 24. Hyolithid sp. MGUH 18.700 from GGU collection 225530, dorsal surface showing ornament, X 8.

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Most specimens described here were located by R. A. Robison in the course of his preparation of GGU samples from the Holm Dal Formation in search of trilobites. Suzanne Maling Hansen prepared most of the photographic prints. Bente Thomas draughted figures. Published with permission from the Director, Geological Survey of Greenland.

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