Palaeontology, stratigraphy and environmental setting of Middle Cambrian outer shelf deposits, North Greenland

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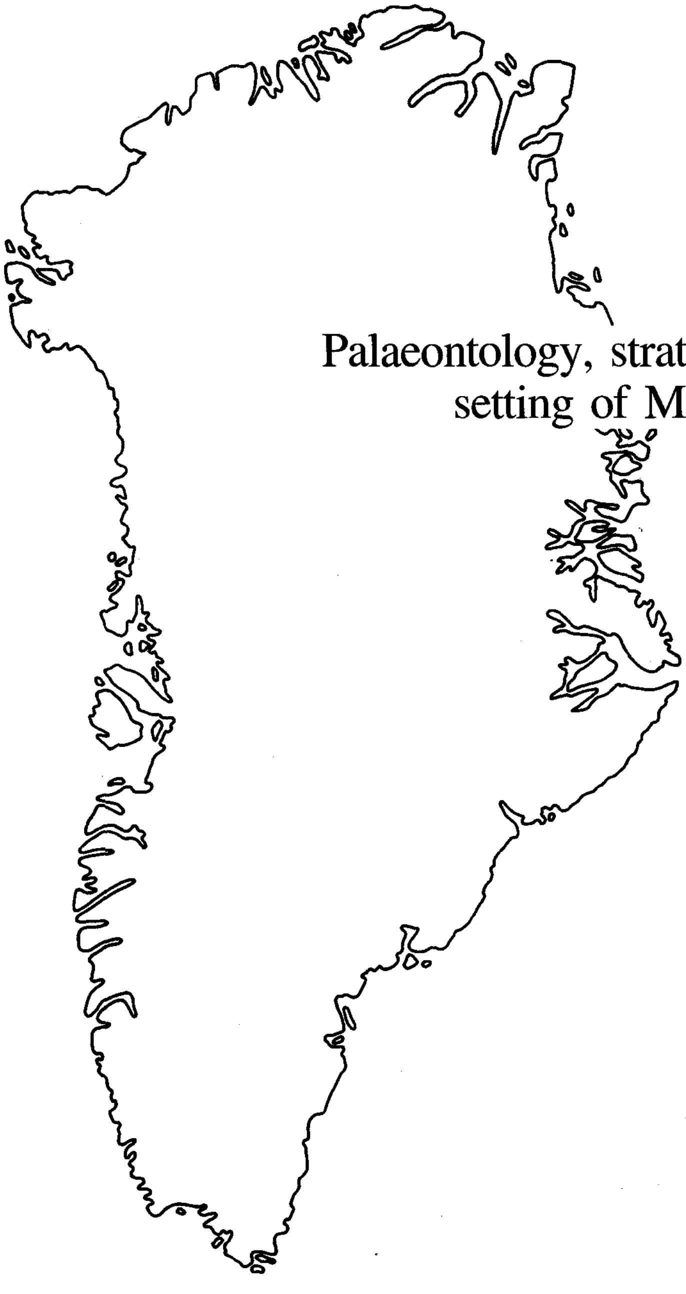

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Middle Cambrian trilobites of Baltic and Laurentian aspect are locally common and diverse in slope apron to deep outer shelf deposits of the Brønlund Fjord and Tavsens Iskappe Groups which are exposed in a narrow belt along the northern coast of western and central North Greenland.

In the first of five papers comprising the present volume, Jon R. Ineson, Finn Surlyk, A. K. Higgins and John S. Peel describe the stratigraphy, facies and depositional setting of these outer shelf sediments which are assigned to the Aftenstjernesø, Henson Gletscher and Kap Stanton Formations (Early Cambrian – Early Ordovician). The first two of these formations are known from the Brønlund Fjord Group in its principal outcrop and type area along the northern margin of the Greenland Inland Ice, but the Kap Stanton Formation (Tavsens Iskappe Group) is formally described herein. Dark, fine-grained sediments dominate, ranging in composition from lime mudstones to cherty calcareous or dolomitic mudstones. Lime grainstones and packstones are locally important, while carbonate breccia beds dominate some sections.

Richard A. Robison describes abundant agnostoid trilobites from the Henson Gletscher Formation and the lower beds of the Kap Stanton Formation, identifying representatives of the *Ptychagnostus gibbus*, *Ptychagnostus atavus* and *Lejopyge laevigata* interval-zones of the Middle Cambrian. Two new genera (*Megagnostus* and *Schismagnostus*) are described, as are five new species: *Agnostus lophotus*, *Diplorrhina oncota*, *Megagnostus diclidus*, *Schismagnostus plicatus* and *Tomagnostus bothrus*.

In the first of two papers, Loren E. Babcock describes Middle Cambrian polymeroid trilobites of Laurentian and Baltic aspect from the Henson Gletscher Formation and the lowermost Kap Stanton Formation. Trilobites of Laurentian aspect were found in lime mudstone and wackestone representing shelf lithofacies, while trilobites of Baltic aspect characterise outer shelf, lime mudstone lithofacies. In addition to the three interval-zones recognised by R. A. Robison, Loren Babcock recognises the Middle Cambrian *Glossopleura* assemblage-zone in strata of the Henson Gletscher Formation devoid of agnostoid trilobites. One new genus (*Costadiscus*) and thirty three species of polymeroid trilobites are described, including the following new species: *Bathyuriscus concavus*, *Costadiscus minutus*, *Dasometopus groenlandicus*, *Elyx trapezoidalis*, *Kootenia nodosa* and *Opsidiscus longispinus*. Loren Babcock employs cladistic analysis to investigate the relationships of eodiscid and paradoxidid trilobite genera. He concludes that the eodiscoids are a paraphyletic and possibly polyphyletic group that did not share a close common ancestor with the agnostoids. Paradoxidids are considered to form a monophyletic group.

In a second paper, Loren E. Babcock demonstrates strong biofacies segregation of polymeroid biofacies near the shelf margin of the Laurentian continent, elucidating the expressions 'Atlantic' and 'Pacific' previously used to express the affinity of trilobite assemblages. Trilobites of Laurentian aspect lived in warm, relatively shallow waters, while cool, deeper waters contained biofacies of Baltic aspect. Polymeroids from the *Glossopleura* and *Ptychagnostus gibbus* zones in the collections from northernmost North Greenland are mainly of Laurentian aspect. Collections from the *Lejopyge laevigata* zone of the Kap Stanton Formation are entirely of Baltic aspect. Mixing of polymeroids of Laurentian and Baltic aspect in collections from the *Ptychagnostus atavus* zone was produced by downslope movement by sediment gravity flows. The segregation of trilobite biofacies is considered as evidence for the existence of a thermocline in marine waters surrounding the Laurentian continent in the Middle Cambrian. In conclusion, Loren Babcock discusses the importance of the correct interpretation of biofacies segregation for analyses of tectonostratigraphic terranes, noting that recognition of cool water assemblages alone is not sufficient evidence to assume that a terrane originated in high latitudes.

John S. Peel describes a single enigmatic fossil from the Henson Gletscher Formation as a new genus and species, *Nyeboeconus robisoni*. Somewhat similar forms have been identified recently as chondrophorine hydrozoans or *Problematica* but the balance of available evidence favours interpretation of *N. robisoni* as a helcionelloid mollusc.

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Grønlands Geologiske Undersøgelse
Ujarassiortut Kalaallit Nunaanni Misissuisoqarfiat
Geological Survey of Greenland

The Geological Survey of Greenland (GGU) is a research institute affiliated to the Mineral Resources Administration for Greenland (MRA) within the Danish Ministry of Energy. As with all other activities involving mineral resources in Greenland, GGU's investigations are carried out within the framework of the policies decided jointly by the Greenland Home Rule Authority and the Danish State.

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Contents

Dansk sammendrag

De nordgrønlandske litologiske enheder, Brønlund Fjord og Hans Tavsens Iskappe Grupper, indeholder rige trilobitfaunaer af mellem-kambrisk alder. De findes i mørke, finkornede sedimenter, som er aflejret på den ydre shelf. En ny formation, Kap Stanton Formationen, er beskrevet.

Der beskrives mere end 70 trilobitarter fra Henson Gletscher og Kap Stanton Formationerne; de 11 er nye arter. Der er ligeledes opstillet og beskrevet 3 nye trilobitslægter, *Megagnostus*, *Schismagnostus* og *Costadiscus*, og en helcionelloid mollusk, *Nyeboeconus robisoni*, er både en ny slægt og en ny art.

Der ses tydeligt flere forskellige samfund af polymeroide trilobitter i det undersøgte materiale, og forskellene tolkes som forskelle i den oprindelige havtemperatur. Samtidige, almindeligt forekommende trilobitter på det nordamerikanske kontinent (Laurentia) levede i varmt, relativt lavt vand omkring Grønland, mens de karakteristiske, mellem-kambriske arter fra østersøområdet (Baltikum) levede i dybere og køligere vand.

Forståelsen af aflejringsmiljøets indflydelse på forskellene mellem trilobitfaunaer i Nordamerika og østersøområdet er kritisk for fortolkningen af kontinentalpladernes tidligere placering baseret på sammenligning af faunaer.

Imaqarnersiuineq

Kalaallit Nunaata Avannaarsuani ujaqqat pinngorsimanerat tunngavigalugu immikkoortinneqarsimasut, Brønlund Fjord aamma Hans Tavsens Iskappe Grupper, uumasunik qalerualinnik ukiut 500-600 milliunit matuma siornatigut ujaranngorsimasunik trilobitinik akoqaqaat. Ujaqqani kinnganerni taartuni aseqqorissaartuni ikkannersuup sivingarngani pinngorsimasuni siumorneqarsinnaapput. Kinnganerit immikkoortumut nutaamut Kap Stanton Formationimik taallugu immikkoortinneqarnissaat paasisat kingulliit tunngavigalugit siunnersuutigineqarpoq, taakkulu qaleriiaarnerat sumilu kiviorarsimanerat allaaserineqarluni.

Immikkoortuni marlunni Henson Gletscherimi Kap Stanton Formationimilu trilobitit assigiinngitsut 70-it sinnerlugit allaaserineqarput; taakkunanilu aqqanillit nutaajullutik. Kiisalu qaleruallit ilaqutaariit nutaat pingasut siumorneqarsimasut allaaserineqarput, tassa *Megagnostus, Schismagnostus* aamma *Costadiscus,* kiisalu alla immikkuullaarissoq nutaaq *Nyeboeconus robisoni.*

Misissorneqartuni ilaqutaariit immap kissassusaanik peqquteqartumik immikkuullaarinnerat takuneqarsinnaavoq. Maannakkut amerikkap avannarliup nunavissuani siumorneqarsinnaasut (Laurentiami) immami kissartumik ikkannerusumi uumasuusimapput, kambriumilli qeqqaata missaani Østersøp imartaaneersut Kalaallit Nunaata Avannaarsuani uumasimasunut naleqqiullugit immami itinerusumi nillernerusumilu uumasuusimallutik.

Amerikkami avannarlermi Østersøllu eqqaani trilobitit sumi uumasimanerisa assigiinngissutaat uumasuusimasut tunngavigalugit nunavissuit qangarssuaq qanoq inissisimanerinut paasiniaanermi pingaaruteqartorujussuuvoq.

Cover picture

Cape north of the island Primus, inner J. P. Koch Fjord. Section includes Aftenstjernesø and Henson Gletscher Formations of the Brønlund Fjord Group (lower crags near fjord) and the Kap Stanton Formation of the Tavsens Iskappe Group (up to crag in middle of section); these are overlain by Ordovician black cherts of the Amundsen Land Group and yellow-weathering turbidites of the Peary Land Group (upper crags).

Slope apron and deep shelf sediments of the Brønlund Fjord and Tavsens Iskappe Groups (Lower Cambrian – Lower Ordovician), North Greenland: stratigraphy, facies and depositional setting

Jon R. Ineson, Finn Surlyk, A. K. Higgins and John S. Peel

During most of the early Palaeozoic, the Franklinian Basin in North Greenland was composed of a southern shelf and a northern deep-water basin. From the late Early Cambrian to the Early Ordovician, the shelf displayed a stepped, terraced profile with two discrete breaks in slope. These occurred at the platform edge and at the boundary between the outer shelf and the deep-water turbidite basin. The transect from platform margin to deep outer shelf is recorded by the carbonate and siliciclastic sediments of the Brønlund Fjord and Tavsens Iskappe Groups (Lower Cambrian – Lower Ordovician). The platform margin and flanking carbonate slope apron are preserved in the southern outcrop belt, trending east–west parallel to the margin of the Greenland Inland Ice. Some 50–100 km farther north, strata of equivalent age reappear in an outcrop belt that follows the northern coastline of western and central North Greenland; these strata document the transition from slope apron to deep-water outermost shelf or upper slope.

In this northern outcrop belt, the Brønlund Fjord Group comprises two formations, the Aftenstjernesø Formation (Lower Cambrian) and the Henson Gletscher Formation (Lower–Middle Cambrian), as defined from the southern outcrop belt. The Tavsens Iskappe Group consists of a single formation defined here as the Kap Stanton Formation (Middle Cambrian – Lower Ordovician). The Brønlund Fjord and Tavsens Iskappe Groups in the northern outcrop belt are dominated by dark-coloured fine-grained sediments ranging in composition from lime mudstones through marlstones to cherty calcareous or dolomitic siliciclastic mudstones. Graded and cross-laminated lime grainstones and packstones are locally important and carbonate breccia beds up to several tens of metres thick dominate some sections and form persistent marker beds at certain stratigraphic levels. These facies record deposition from suspension, mud-rich turbidity currents, slides and debris flows in a slope apron to deep shelf setting.

The northern outcrop belt of the Brønlund Fjord and Tavsens Iskappe Groups represents an oblique section through the Cambrian outer shelf from proximal slope apron in the west to deep outermost shelf in the east. Although the western platform margin is not exposed, these deeper-water shelf deposits testify to a history of intermittent platform progradation during the Middle and early Late Cambrian followed by aggradation of the platform during the latest Cambrian and the Early Ordovician.

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Cambrian platform margin and outer shelf deposits in North Greenland are best known from the extensive southern outcrop belt along the northern margin of the Inland Ice (Fig. 1; see Ineson & Peel, 1987; Surlyk &

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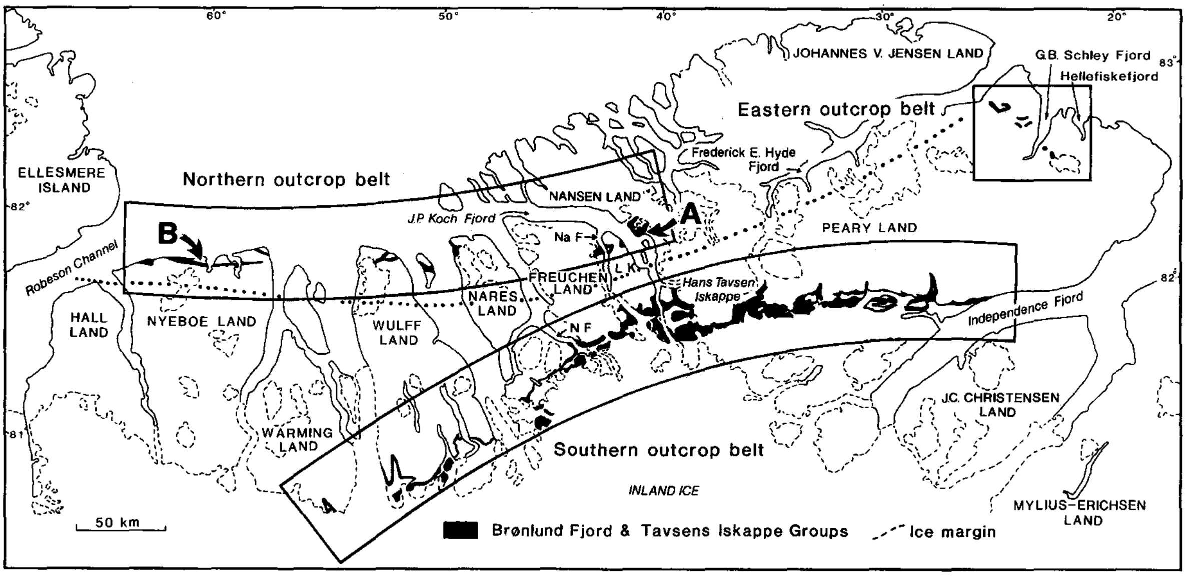


Fig. 1. Sketch map showing the distribution of the Brønlund Fjord and Tavsens Iskappe Groups in North Greenland. These strata crop out in three discrete areas: the southern, eastern and northern outcrop belts. The dotted line marks the position of the Navarana Fjord lineament. A and B show the location of the sections in Fig. 5 (see also Fig. 12). LK, Lauge Koch Land; NaF, Navarana Fjord; NF, Nordenskiöld Fjord. Localities in north Nyeboe Land shown in Fig. 7.

Ineson, 1987; Higgins *et al.*, 1991a, b). However, contemporaneous strata also crop out in an east–west belt parallel to the northern coastline of western and central North Greenland (Fig. 1), in the cores of a series of open to tight anticlinal folds and in thrust slices (Higgins & Soper, 1985; Higgins *et al.*, 1992). The sediments exposed in this outcrop belt were deposited on the deeper-water, more distal portion of the Cambrian shelf, near the transition to the basin slope. With the exception of the northernmost, allochthonous sections, these strata are readily assigned to the Brønlund Fjord and Tavsens Iskappe Groups as defined from the southern outcrop belt (Peel, 1979a; Ineson & Peel, 1980; Ineson, 1988; Ineson & Peel, unpublished).

The aim of this paper is to present a review of the stratigraphy and regional depositional setting of the Brønlund Fjord and Tavsens Iskappe Groups in their northern outcrop to act as an introduction to the detailed taxonomic and biostratigraphic studies that follow in this volume (Babcock, 1994a, b; Robison, 1994; Peel, 1994). In addition, the Kap Stanton Formation, a new formation of the Tavsens Iskappe Group, is formally defined. In particular, the aim is to clarify the relationship between these northern sections and the better known, more proximal shelf sediments of the southern outcrop belt (Fig. 1).

Regional setting

During the early Palaeozoic, North Greenland formed part of the Franklinian Basin which extended westwards into Arctic Canada. In Greenland, the preserved basin fill stretches almost 1000 km from east to west and 200 km from north to south. The succession is about 8 km thick and is essentially of early Palaeozoic age, although possibly extending down into the latest Proterozoic and up into the earliest Devonian.

The outcrop pattern of the Lower Palaeozoic broadly parallels the east–west coastline of North Greenland. Archaean crystalline basement and overlying Proterozoic sedimentary strata crop out along the fringes of the Inland Ice in the south and east. Succeeding Lower Palaeozoic strata occupy most of the remaining ice-free terrain. Outliers of Late Palaeozoic and Mesozoic age unconformably overlie the Franklinian Basin strata in eastern areas of North Greenland (see Stemmerik & Håkansson, 1991, Håkansson *et al.*, 1991). Rocks of the Franklinian Basin are largely undeformed in the south; the degree of deformation increases northwards and the metamorphic grade is amphibolite facies in northernmost North Greenland; details of the structure and metamorphic history are given in Higgins *et al.* (1985) and Soper & Higgins (1990).

The full evolutionary history of the Franklinian Basin in North Greenland is given in some detail in recent review articles (Higgins *et al.*, 1991a, b); a brief description is given here with emphasis on the Cambrian shelf.

For much of the early Palaeozoic, the basin consisted of two discrete depositional elements: a shelf to the south, bordering the craton, passing northwards into a deep-water trough. The position and nature of the transition from shelf to trough varied during the early Palaeozoic (Hurst & Surlyk, 1983; Surlyk & Hurst, 1983, 1984). In certain periods (e.g. Early Cambrian, Late Ordovician – Early Silurian), the entire shelf region was the site of shallow-water carbonate sedimentation and the shelf-to-trough transition was an abrupt, often precipitous scarp (see Surlyk & Ineson, 1987, 1992; Peel *et al.*, 1992). At other times (e.g. late Early Cambrian), the shelf was dominated by siliciclastic sediments and showed a typical continental shelf profile with a shelf-slope break in several hundred metres of water. Intermediate profiles were also represented, for example from the late Early Cambrian to the earliest Ordovician, during which time a shallow-water carbonate platform occupied the southern inner region of the shelf, grading northwards onto the mixed carbonate-siliciclastic outer shelf which in turn passed abruptly into the deep-water trough.

The position of the shelf-to-trough transition follows a number of roughly east–west lineaments. These features probably represent deep-seated faults or monoclines which became successively active during the early Palaeozoic resulting in backstepping of the shelf margin. Thus, from the earliest Cambrian to the Early Ordovician, the shelf margin followed a line from Frederick E. Hyde Fjord through outer J. P. Koch Fjord and north of the present Wulff Land – Nyeboe Land coastline (Fig. 1). In the Early Ordovician, the margin shifted southwards to the Navarana Fjord lineament which proceeded to control the position of the carbonate platform margin until the late Llandovery. At this time, the outer platform foundered and basinal sediments progressively onlapped the shelf, with ultimate drowning of the preserved shelf at the Llandovery–Wenlock boundary. Deep-water sedimentation continued over North Greenland until at least the

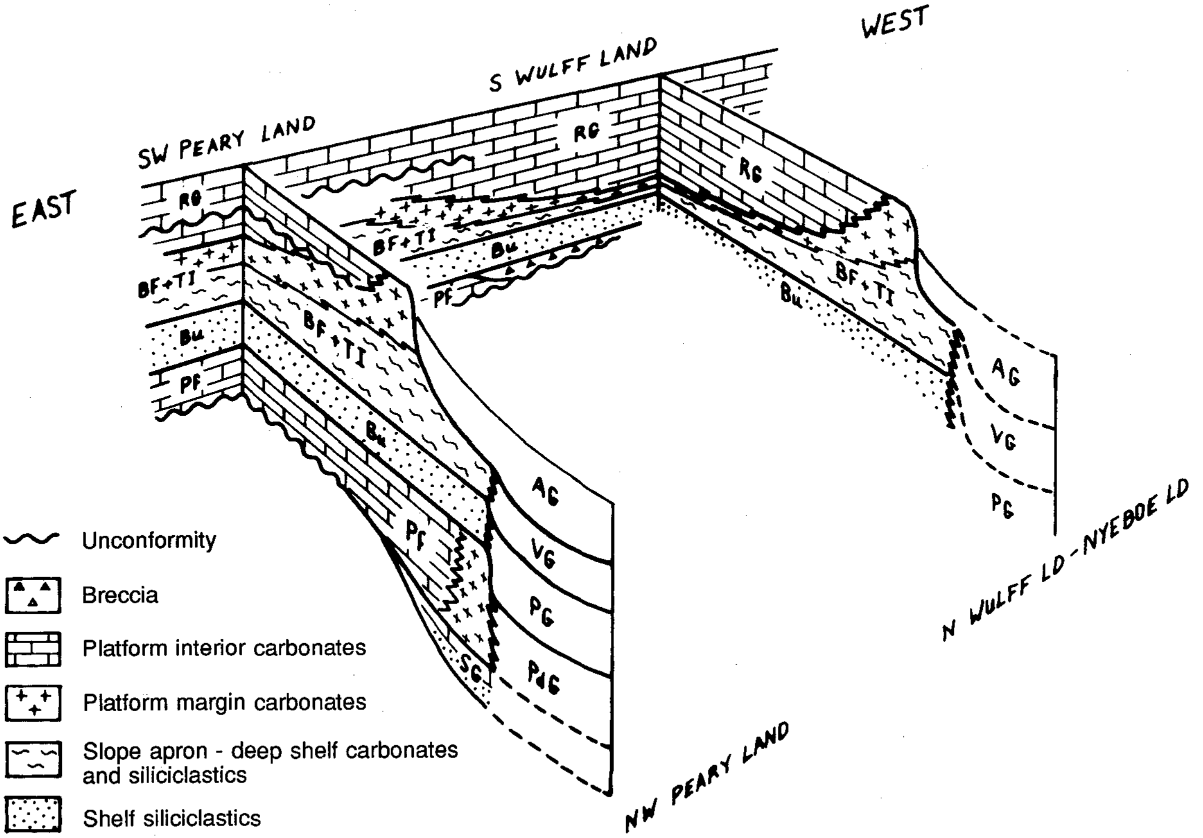


Fig. 2. Fence diagram (view from north) showing the regional stratigraphy of the Cambrian shelf and deep-water trough. SG, Skagen Group; Pf, Portfjeld Formation; PdG, Paradisfjeld Group; Bu, Buen Formation; PG, Polkorridoren Group; BF, Brønlund Fjord Group; TI, Tavsens Iskappe Group; RG, Ryder Gletscher Group; VG, Vølvedal Group; AG, Amundsen Land Group.

latest Silurian; the Franklinian Basin was uplifted and deformed in the mid-Palaeozoic Ellesmerian orogeny.

Stratigraphic framework and shelf evolution

The Cambrian sedimentation history of the North Greenland shelf from Peary Land in the east to Nyeboe Land in the west (Fig. 1) is recorded by the Skagen Group (?lowermost Cambrian), the Portfjeld and Buen Formations (Lower Cambrian) and the Brønlund Fjord, Tavsens Iskappe and Ryder Gletscher Groups (Lower–Upper Cambrian; Fig. 2). In recent reviews (Higgins *et al.*, 1991a, b), Cambrian shelf evolution has been considered in terms of four stages.

The mixed carbonate-siliciclastic Skagen Group, representing Stage 1 of Higgins *et al.* (1991a, b) is recognised in isolated exposures from north-east Peary Land, in the east, to northern Wulff Land, in the west (Figs 1, 2); it records deposition on a storm-dominated shelf following the initial transgression of Proterozoic basement. The succeeding Portfjeld Formation (Stage 2), however, extends widely over central areas of North Greenland and records the development of a shallow-water carbonate platform over much of the Franklinian shelf in North Greenland (Fig. 3). At the northern limit of the shelf, the platform was fringed by a belt of carbonate sands and stromatolitic mounds, deposited under turbulent, energetic conditions; the margin was a steep escarpment, at least in its latter stages (Higgins *et al.*, 1991a; Peel *et al.*, 1992).

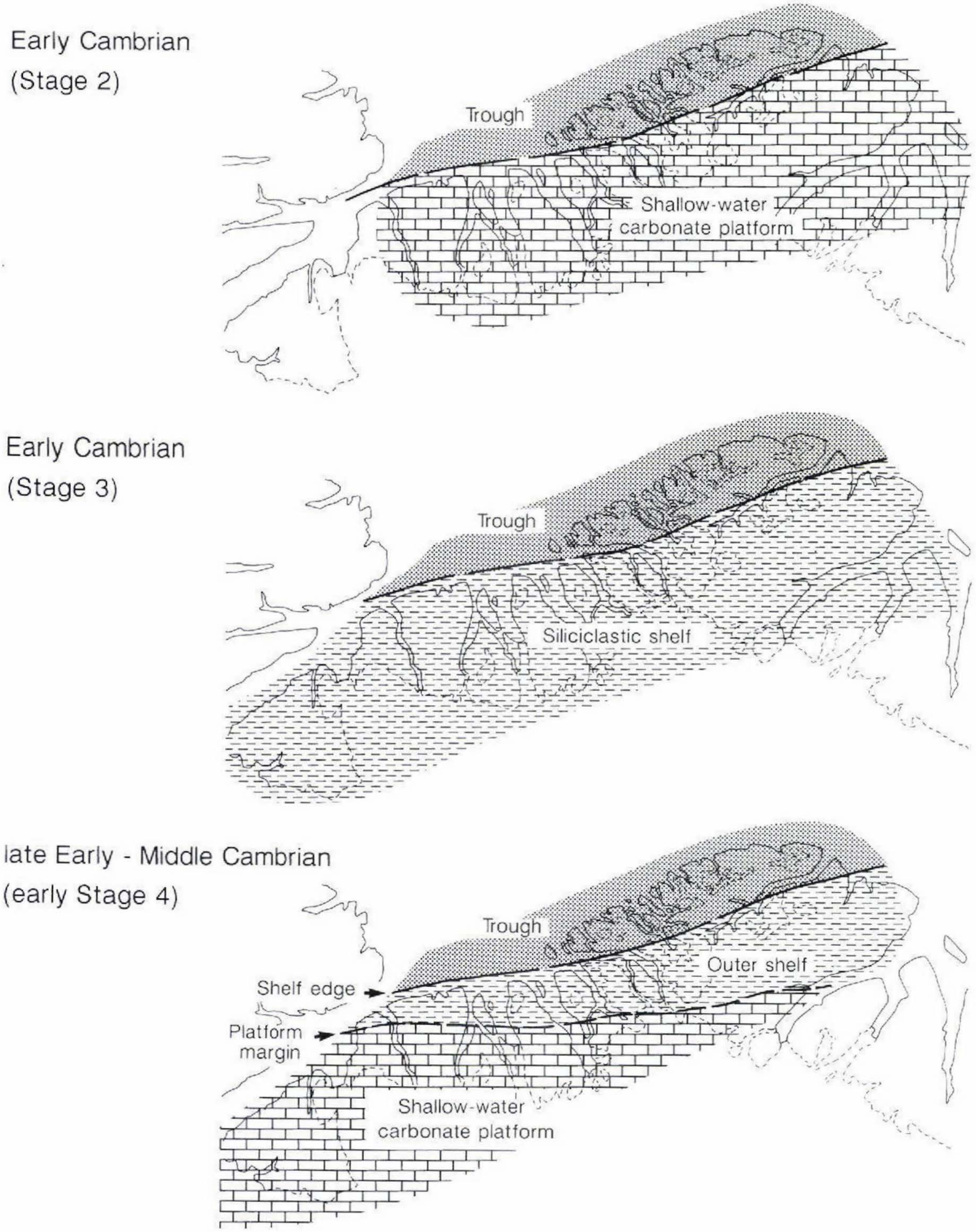
Following exposure and karstification of the platform, the shelf was transgressed; the siliciclastic shelf strata deposited during this episode (Stage 3; Fig. 3) are assigned to the Buen Formation which is recognised throughout central and east North Greenland and can be correlated with similar siliciclastic formations in westernmost North Greenland.

The mud-dominated deep shelf strata of the upper Buen Formation are succeeded abruptly by carbonates of late Early Cambrian age; this boundary heralds the development of a major early Palaeozoic carbonate platform that ultimately decked the entire Franklinian shelf and may have been connected with the East Greenland carbonate platform on the Iapetus margin of Laurentia. During the early phases of its development (Stage 4), however, the shallow-water platform was restricted to the southern, inner portion of the shelf and passed northwards into a deeper-water outer shelf setting (Fig. 3). The deep shelf, in turn, graded northwards into the deep-water trough. The precise nature of the shelf-to-trough transition at this time is unknown. Although demonstrably a steep scarp with considerable relief during the latter part of Stage 2 and early Stage 3 (upper Portfjeld and lower Buen Formations, see above), differential subsidence across this structural lineament may have been less important and the transition more subdued by latest Early Cambrian times. The contrast in thickness between the outermost shelf deposits and the basinal Vølvedal Group, however, indicates that significant relief persisted at this margin throughout the Cambrian and into the Ordovician (see Friderichsen *et al.*, 1982; Higgins *et al.*, 1991a, b, 1992).

The fundamental subdivision of the shelf environment during the Cambrian is reflected in the stratigraphic scheme (Fig. 2): platform interior rocks are assigned to the Ryder Gletscher Group whereas platform margin, carbonate slope apron and deep shelf strata are assigned to the Brønlund Fjord and Tavsens Iskappe Groups. The deeper-water outer shelf sediments grade southwards and up-section into platform margin and platform interior facies reflecting a general northward progradation of the platform during the Cambrian (Fig. 2).

This simple south to north progradational pattern, however, does not explain the east–west variation in the Cambrian stratigraphy (see Figs 2, 4). In western and much of central North Greenland, the shelf subsided uniformly from the Early Cambrian to the Early Silurian, accumulating a thick and essentially conformable succession of platform carbonates. In contrast, the eastern margin of the North Greenland craton experienced uplift during the Middle and Late Cambrian, probably in response to an early collisional event along the western margin of the Iapetus Ocean (Surlyk & Hurst, 1984; Surlyk, 1991). This resulted in progressive exposure of eastern shelf areas during the Cambrian and the development of a regional unconformity at the base of the Wandel Valley Formation (uppermost Lower–Middle Ordovician; Fig. 2). Uplift was greatest in magnitude and duration in the east so that the hiatus decreases in stratigraphic importance westwards and is not recognised farther west than Nares Land (Figs 1, 2).

Thus, in the southern outcrop belt (Fig. 1), the Brønlund Fjord, Tavsens Iskappe and Ryder Gletcher Groups record northward progradation of shallow-water carbonate sediments over outer shelf deposits. In eastern areas, the platform became progressively emergent during the Cambrian and platform interior facies (i.e. Ryder Gletscher Group) are only locally preserved beneath the Wandel Valley Formation basal unconformity (Fig. 2). In western North Greenland and adjacent areas of central North Greenland, however, the outer shelf, slope apron and platform margin deposits of the Brønlund Fjord Group, and by inference the Tavsens Iskappe Group, are conformably succeeded by Cambro-Ordovician platform carbonates assigned to the Ryder Gletscher Group (Fig. 2).



Early Cambrian (Stage 2)

Early Cambrian (Stage 3)

late Early - Middle Cambrian (early Stage 4)

Fig. 3. Cambrian palaeogeography of North Greenland; see text for discussion. The position of the Cambrian shelf edge is extrapolated westwards from the exposed margin of the Portfjeld Formation platform (Stage 2) in north-west Peary Land; the inferred basin slope deposits (Stages 3, 4) occurring in thrust slices along the northern coastlines of Nares Land, Wulff Land and Nyeboe Land (see Higgins *et al.*, 1992) are not incorporated in this simplified reconstruction.

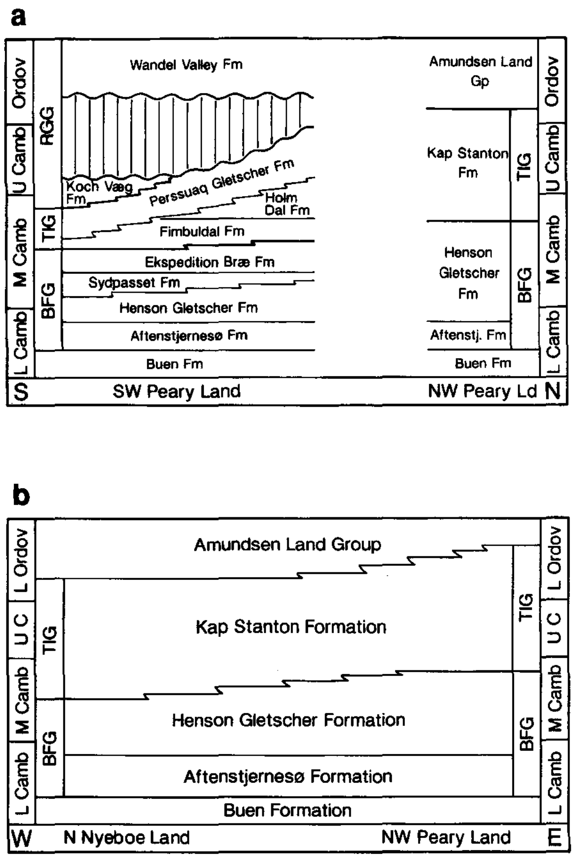


Fig. 4. Lithostratigraphy of the Brønlund Fjord (BFG) and Tavsens Iskappe Groups (TIG) in (a) a south-to-north transect in west Peary Land and (b) a west-to-east transect in the northern outcrop belt (see Fig. 1). RGG, Ryder Gletscher Group.

In the northern outcrop belt from outer J. P. Koch Fjord to northern Nyeboe Land (Fig. 1), the carbonate slope apron and deep, outer shelf sediments of the Brønlund Fjord and Tavsens Iskappe Groups were deposited basinward of the maximum northernmost extent of the platform (Fig. 2). They are overlain by black, cherty, graptolitic mudstones of Early Ordovician age, reflecting a shift in the position of the trough margin in the Early Ordovician from north of the northern coastline of central areas of North Greenland to the Navarana Fjord lineament (Figs 1, 2, 3). The easternmost sections of the northern outcrop belt, in Navarana Fjord and outer J. P. Koch Fjord, can be readily correlated with the southern outcrop belt since the transition from platform to outer shelf is superbly exposed in these southern exposures (see Ineson & Peel, 1980, 1987; Higgins *et al.*, 1991a, b). West of Nordenskiöld Fjord (Fig. 1), however, this transition is not exposed; platform carbonates dominate the southern outcrop and outer shelf facies make up the northern outcrop belt, the intervening margin being buried beneath younger strata. The evolution of the platform margin in this western area is discussed further below.

Lithostratigraphy

Three formations are assigned to the Brønlund Fjord and Tavsens Iskappe Groups in the northern outcrop belt; these are equivalent to the lower three units of the four part Cambrian – Lower Silurian starved basin sequence described by Higgins & Soper (1985). The lower two formations, overlying the Buen Formation (Figs 2, 4), are assigned to the Aftenstjernesø and Henson Gletscher Formations of the Brønlund Fjord Group, as defined from the southern outcrop belt (Ineson & Peel, unpublished; see also Higgins *et al.*, 1991a, b). The third formation is defined here as the Kap Stanton Formation, a new formation of the Tavsens Iskappe Group; this formation is succeeded by the Amundsen Land Group, defined from a more basinal setting by Friderichsen *et al.* (1982). Detailed stratigraphic data from this Cambrian–Ordovician outcrop belt were recently presented by Higgins *et al.* (1992). Brief descriptions of the typical facies of the respective formations are included here, together with an interpretation of the broad depositional setting.

Brønlund Fjord Group

Aftenstjernesø Formation

Description. At the type section in southern Lauge Koch Land (Fig. 1; Ineson & Peel, unpublished), the Aftenstjernesø Formation comprises *c.* 62 m of dolomites that include glauconitic, phosphoritic grainstones and packstones, carbonate turbidites, nodular and laminated dolomites and carbonate breccia beds. In its northern outcrop, from outer J. P. Koch Fjord, western Peary Land to northern Nyeboe Land (Fig. 1), the Aftenstjernesø Formation is typically 25–50 m thick (Figs 5, 6), although anomalously thick sections have been recorded locally (e.g. *c.* 80 m in north-east Nyeboe Land; Higgins *et al.*, 1992). In north-south transects, the formation thins slightly northwards (see Higgins *et al.*, 1992, fig. 4).

The base of the formation is typically sharp and is marked by a thin rusty-weathering interval of pyritic, phosphoritic dolomitic limestones that include nodular mudstones and wackestones and skeletal, intraclastic packstones and grainstones. This unit, which is equivalent to 'Member A' of the Aftenstjernesø Formation in its southern outcrop (see Frykman, 1980), forms a readily recognisable marker bed, about 1 m thick, in eastern sections (Fig. 6a) above the dark greenish-grey siliciclastic mudstones of the Buen Formation. In western sections, this unit may be thicker and the boundary more

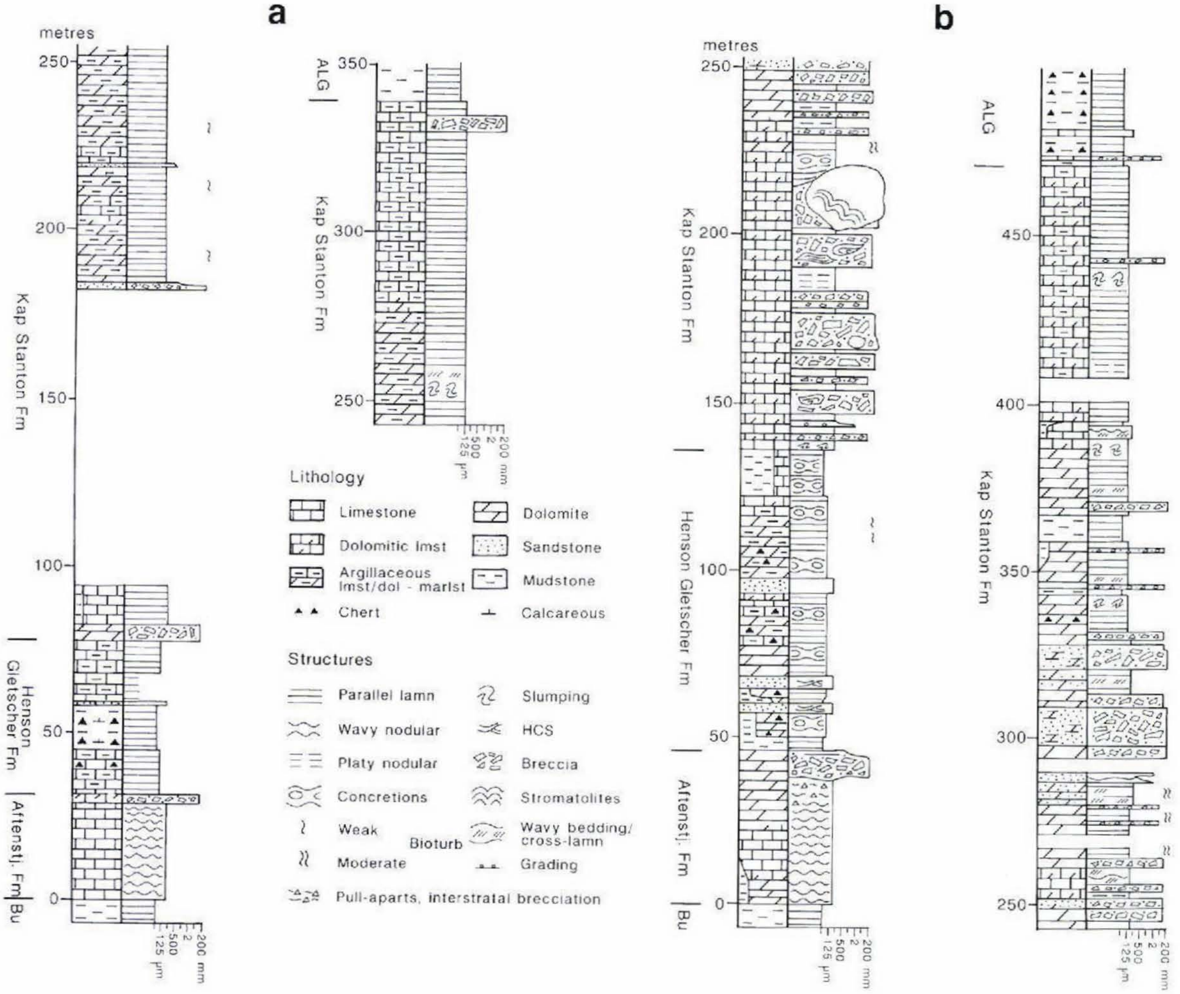


Fig. 5. Stratigraphic sections through the Brønlund Fjord and Tavsens Iskappe groups in the northern outcrop belt. a, outer J. P. Koch Fjord; b, Hand Bugt, northern Nyeboe Land (see Fig. 1). The legend also applies to Fig. 8. Bu, Buen Formation; Aftenstj., Aftenstjernesø; ALG, Amundsen Land Group.

gradational in character (see Fig. 5b). Above this basal marker, the formation is dominated by nodular, thin-bedded, argillaceous, dark grey or black lime mudstones or dolomites. Parallel lamination is commonly evident and cross-lamination is observed locally in rare graded limestone beds. The formation is capped by a highly persistent, clast-supported carbonate breccia bed, up to 20 m thick, which forms a characteristic marker bed throughout the northern outcrop of the Aftenstjernesø Formation (Figs 5, 6; Higgins *et al.*, 1992). A closely comparable and probably correlative mass-flow breccia bed caps the Aftenstjernesø Formation over much of the southern outcrop belt (see Ineson, 1980, 1985; Ineson & Peel, unpublished).

Boundaries and age. The carbonate-dominated Aftenstjernesø Formation conformably overlies fine-grained siliciclastics of the Buen Formation as in the southern outcrop belt (Ineson & Peel, 1980; unpublished); the boundary is marked by a distinctive pyritic, phosphoritic horizon or interval (see Fig. 6). The top of the formation is defined at the top of a laterally persistent carbonate mass-flow breccia sheet that marks a shift from the carbonate-dominated Aftenstjernesø Formation to the black cherty calcareous mudstones and argillaceous lime mudstones of the Henson Gletscher Formation.

In its southern outcrop, the Aftenstjernesø Formation is assigned a late Early Cambrian age; the basal beds yield a diverse fauna indicative of the *Bonnia–Olenellus* Zone (Palmer & Peel, 1979; Bendix-Almgreen & Peel, 1988). Similarly, in the northern outcrop belt, fossils are generally only present in the lowermost beds which have

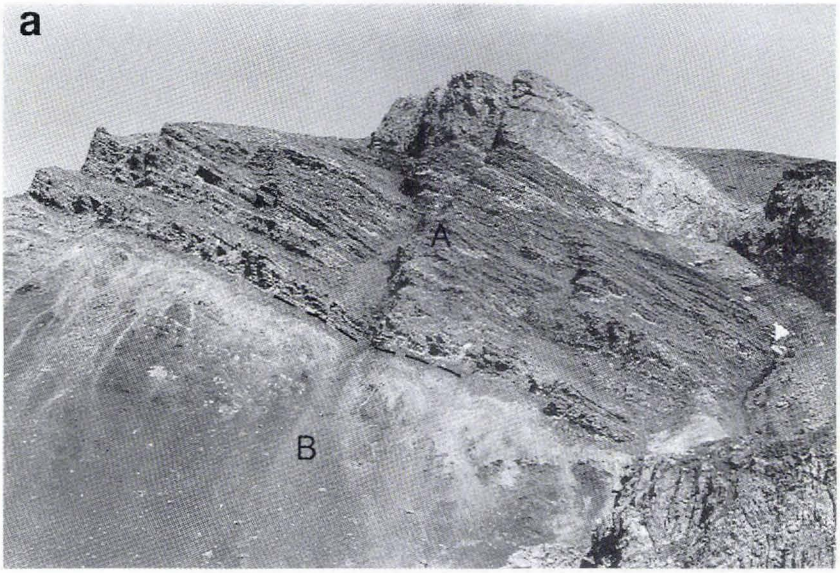


Fig. 6a. Aftenstjernesø Formation (A) overlying the poorly exposed Buen Formation (B). Note the light-coloured scree emanating from the base of the Aftenstjernesø Formation; this reflects the presence of the distinctive pyritic marker bed at the base of the formation. Note also the massive carbonate breccia bed (*c.* 7 m thick) capping the formation. East side of Navarana Fjord.

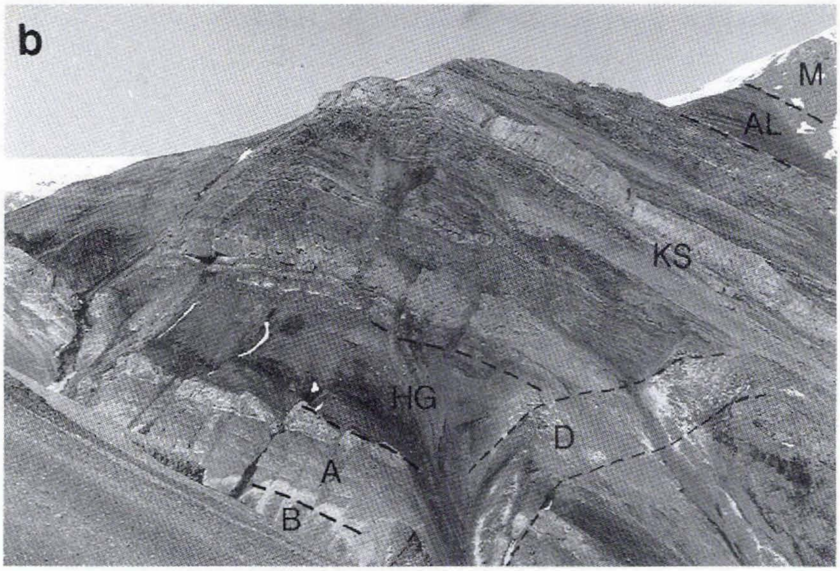


Fig. 6b. Dark-coloured Cambrian and Ordovician strata capped by pale sandstone turbidites of the Lower Silurian Merqujôq Formation (M). B, Buen Formation (Lower Cambrian); A, Aftenstjernesø Formation (Lower Cambrian); HG, Henson Gletscher Formation (Lower–Middle Cambrian); KS, Kap Stanton Formation (Middle Cambrian – Ordovician); AL, Amundsen Land Group (Ordovician); D, Tertiary dyke. East side of Navarana Fjord. Aftenstjernesø Formation is *c.* 30 m thick.

yielded the coeloscleritophoran *Chancelloria* and hyolithids at a number of localities. An atypically thick section in north-east Nyeboe Land, however, is richly fossiliferous throughout the formation. The fauna includes olenellid and eodiscid trilobites, associated with the helcionelloid mollusc *Latouchella*, dermal sclerites of the palaeoscolecidan worm *Hadimopanella* and inarticulate brachiopods (Peel, 1974, 1979b; Dawes & Peel, 1984; Peel & Larsen, 1984; Higgins *et al.*, 1992). Blaker (1991) described *Serrodiscus speciosus* (Foord, 1873) [= *S. bellimarginatus* of Dawes, 1976, p. 277 and Peel, 1979b, p. 116], together with *S. daedalus* Öpik, 1975, *S.*? *latus* Rasetti, 1966 and *Olenellus* sp. A late Early Cambrian age is indicated and the boundaries of the Aftenstjernesø Formation are considered to be essentially isochronous throughout both the northern and southern outcrop areas.

Facies and depositional environment. The dominant facies, comprising thin-bedded, nodular, argillaceous lime mudstones, typically shows parallel lamination and was deposited largely out of suspension, both from the water column and from starved muddy turbidites. Bioturbation is rare, indicating poorly-oxygenated bottom conditions. Rare thin graded, cross-laminated packstones and wackestones record the episodic incursion of more energetic turbidity currents bearing carbonate sand and silt. The thick, clast-supported, unstratified carbonate breccia bed capping the formation has a dolomitised carbonate mud matrix, indicating deposition from a viscous debris flow (see Ineson, 1980, 1988).

The Aftenstjernesø Formation in the northern outcrop belt records deposition primarily of hemipelagic lime mud in an oxygen-starved, sub-wavebase, low energy environment. The scarcity of sand-grade turbidites and coarse debris flow deposits indicates deposition in a distal, outer shelf setting beyond the depositional range of much of the coarser sediment gravity flows derived from the advancing platform and slope apron (see Ineson, 1980, 1985; Higgins *et al.* 1991a, b).

Henson Gletscher Formation

Description. The Henson Gletscher Formation forms a dark grey or black, recessive-weathering interval sandwiched between the more resistant carbonates of the Aftenstjernesø and Kap Stanton Formations (Figs 5, 6b). It is commonly between 20 m and 60 m thick but attains some 90 m in northern Nyeboe Land (Fig. 5b).

In its southern outcrop, the Henson Gletscher Formation is characterised by dark, organic-rich argillaceous lime mudstones and dolomites with a distinctive sandstone unit in the middle of the formation that thickens southwards (Ineson & Peel, 1980, 1987, unpublished; Christiansen *et al.*, 1987). In the northern outcrop belt, the formation is carbonate-starved relative to the southern succession, being composed mainly of black, calcareous or dolomitic, shaly mudstones and black cherts with subordinate spicular argillaceous lime mudstones or dolomites. The proportion of carbonate increases westwards and the Henson Gletscher Formation in northern Nyeboe Land (Fig. 5b) is strongly reminiscent of the type section in Lauge Koch Land (see fig. 22 in Ineson, 1980). At Hand Bugt (Fig. 5b), thin beds and laminae of skeletal packstone occur at certain levels in the upper half of the formation (see Babcock, 1994a, b).

Sandstones are present in many sections through the Henson Gletscher Formation in the northern outcrop belt but are best developed in northern Wulff Land and Nyeboe Land (Fig. 5b). These white, pale grey or yellow sandstones are very fine-grained to fine-grained; beds are typically 20–80 cm thick and the sandstones characteristically form discrete 3–4 m thick units interbedded with dark carbonates or cherty mudstones (Fig. 5b). Individual sandstone beds are sheet-like over a few tens of metres but often pinch and swell. They are internally structureless or show sub-parallel or gently undulating lamination. Dish structures were observed locally and hummocky cross-stratification was identified in northern Nyeboe Land (Fig. 5b).

Boundaries and age. The Henson Gletscher Formation conformably overlies the Aftenstjernesø Formation (Figs 5, 6); the boundary is sharp although locally irregular and is placed where black, cherty shaly carbonates or mudstones overlie the prominent carbonate breccia bed at the top of the Aftenstjernesø Formation (Fig. 6a). The top of the formation is placed where the recessive-weathering dark carbonates and mudstones are succeeded by a more prominent, yellow-brown weathering carbonate-dominated succession assigned to the Kap Stanton Formation (Fig. 6b). The basal beds of the latter formation commonly consist of thin-bedded, nodular lime mudstones or dolomites or, at a number of localities, the base is marked by a carbonate breccia bed (Fig. 5a).

The formation is typically poorly fossiliferous in eastern sections in the northern outcrop belt; indeterminate agnostoid trilobites were collected from the upper third of the formation in outer J. P. Koch Fjord (Fig. 5a; locality 3 in fig. 1 of Babcock, 1994a, b and Robison, 1994). The overlying Kap Stanton Formation yielded rich latest Middle Cambrian faunas (*Lejopyge laevigata* Zone) at this locality, some 10–20 m above the top of the Henson Gletscher Formation (see Babcock, 1994a, b; Robison, 1994), suggesting that the uppermost beds of the formation are of late Middle Cambrian age in these eastern sections.

In northern Nyeboe Land, in the west, rich trilobite faunas were collected from a number of levels in the Henson Gletscher Formation (locality 1, fig. 1 of Babcock, 1994a, b and Robison, 1994). These faunas, which are reported in detail in this volume (see Babcock, 1994a, b; Robison, 1994; Peel, 1994), occur within the upper two-thirds of the formation. The lower third of the formation is unfossiliferous but is probably of late Early Cambrian age, by analogy with the Henson Gletscher Formation in the southern outcrop belt (Ineson & Peel, unpublished).

The lowest of the faunas in the Hand Bugt section occurs at 88 m in the section, some 5 m below the uppermost sandstone bench (Fig. 5b); this fauna is indicative of an early Middle Cambrian age (*Glossopleura* Zone; Babcock, 1994a). In addition to polymeroid trilobites, this horizon has also yielded the helcionelloid mollusc *Latouchella arguta* (Resser, 1939), originally described from the lower Middle Cambrian of the Wasatch Mountains (Resser, 1939).

Succeeding collections, at 102 m and 117–119 m indicate respectively the *Ptychagnostus gibbus* and *P. atavus* Zones of the medial Middle Cambrian (Babcock, 1994a; Robison, 1994). At 102 m, a diverse trilobite fauna is accompanied by elkaniid and acrotretid brachiopods (Lars E. Holmer, personal communication, 1993) and the mollusc *Pelagiella*. In an accompanying paper,

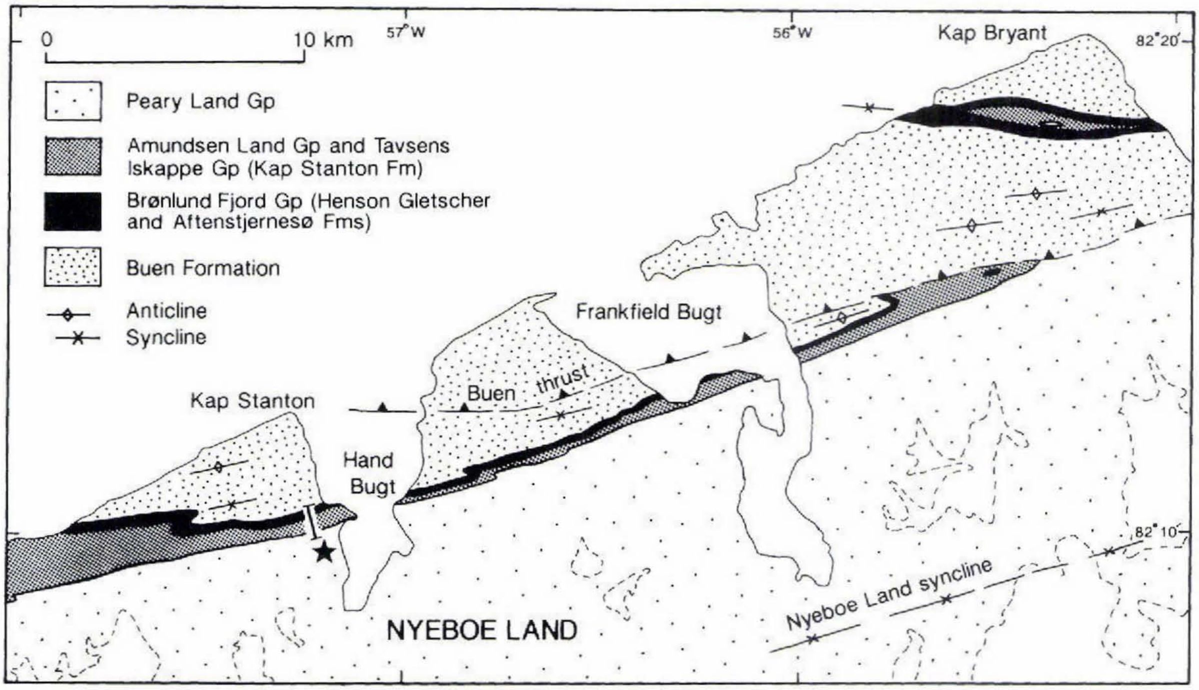


Fig. 7. Sketch map of Hand Bugt, northern Nyeboe Land, showing the location (star) of the type section of the Kap Stanton Formation.

Peel (1994) describes the enigmatic *Nyeboeconus robisoni* gen. et sp. nov. from this horizon. It should be noted that in the southern outcrop belt, the sandstone-dominated interval in the middle of the Henson Gletscher Formation is thought to be wholly of Early Cambrian age; *Bonnia–Olenellus* faunas were recorded from beneath, within and locally immediately above the sandstone interval whereas Middle Cambrian (*P. gibbus* Zone) faunas first appear some 5–10 m above the top of the sandstone unit. Early Middle Cambrian (*Glossopleura* Zone) faunas, however, have not been located in the southern outcrop belt.

Late Middle Cambrian faunas were not recorded from the Henson Gletscher Formation in these western sections, suggesting that the boundary between the Henson Gletscher and Kap Stanton Formations is markedly diachronous in this outcrop belt, younging eastwards. This may reflect the oblique nature of the section through the deep shelf facies belts provided by the northern outcrop belt, such that the western sections record a more proximal setting relative to the platform than the eastern sections (see discussion below).

The marked diachroneity of the top of the Henson Gletscher Formation passing away from the platform is illustrated further by comparing the type section in the southern outcrop belt at the head of J. P. Koch Fjord with the section to the north (locality 3 in fig. 1 of Babcock, 1994a, b and Robison, 1994) in the outer stretches of the fjord (Figs 1, 5a). The boundary falls in the *P. gibbus* Zone of the medial Middle Cambrian in the former section and is of latest Middle Cambrian age (*L. laevigata* Zone) in the latter. The successive northward pinchout of carbonate slope apron wedges leads to the amalgamation of dark, argillaceous, carbonate-starved deep shelf successions which are assigned *en masse* to the Henson Gletscher Formation (Fig. 4a).

Facies and depositional environment. The Henson Gletscher Formation is a recessive-weathering, carbonate-starved succession in relation to the Aftenstjernesø Formation beneath and the Kap Stanton Formation above. It is dominated by black shaly mudstones and variably dolomitised marlstones and argillaceous lime mudstones. These facies show well-developed parallel lamination, often defined by variation in carbonate or silt content; carbonate concretions are common. Laminae and thin beds of skeletal packstone occur at certain levels. Black chert forms discrete beds and nodules, and sponge spicules are common. Bioturbation is very rare. This facies represents deposition of clay and subordinate lime mud primarily from suspension; the thin coarser beds and laminae probably represent deposition from dilute turbidity currents or possibly storm currents. The well-sorted, fine-grained sandstone sheets have sharp, locally erosive bases and, although typically structureless, may show dish structures, diffuse parallel stratification and hummocky cross-stratification; deposition was from bottom-hugging sandy density currents probably initiated by storms.

Deposition of the Henson Gletscher Formation in the northern outcrop belt occurred in a low-energy sub-wave-base environment in a carbonate-starved outer shelf setting. The high organic content, parallel-lamination and scarcity of bioturbation indicates oxygen-deficient bottom conditions. An influx of siliciclastic sand into the outer shelf environment occurred at around the Early–Middle Cambrian boundary.

Tavsens Iskappe Group

Kap Stanton Formation

(new formation)

History. The formation has been previously referred to as the 'dolomite unit', the third of four units making up the 'Cambrian – Lower Silurian starved basin sequence' (Higgins & Soper, 1985). The lower two of these units are assigned to the Aftenstjernesø Formation and Henson Gletscher Formation as described above; the fourth, uppermost unit is assigned to the Amundsen Land Group of Friderichsen *et al.* (1982).

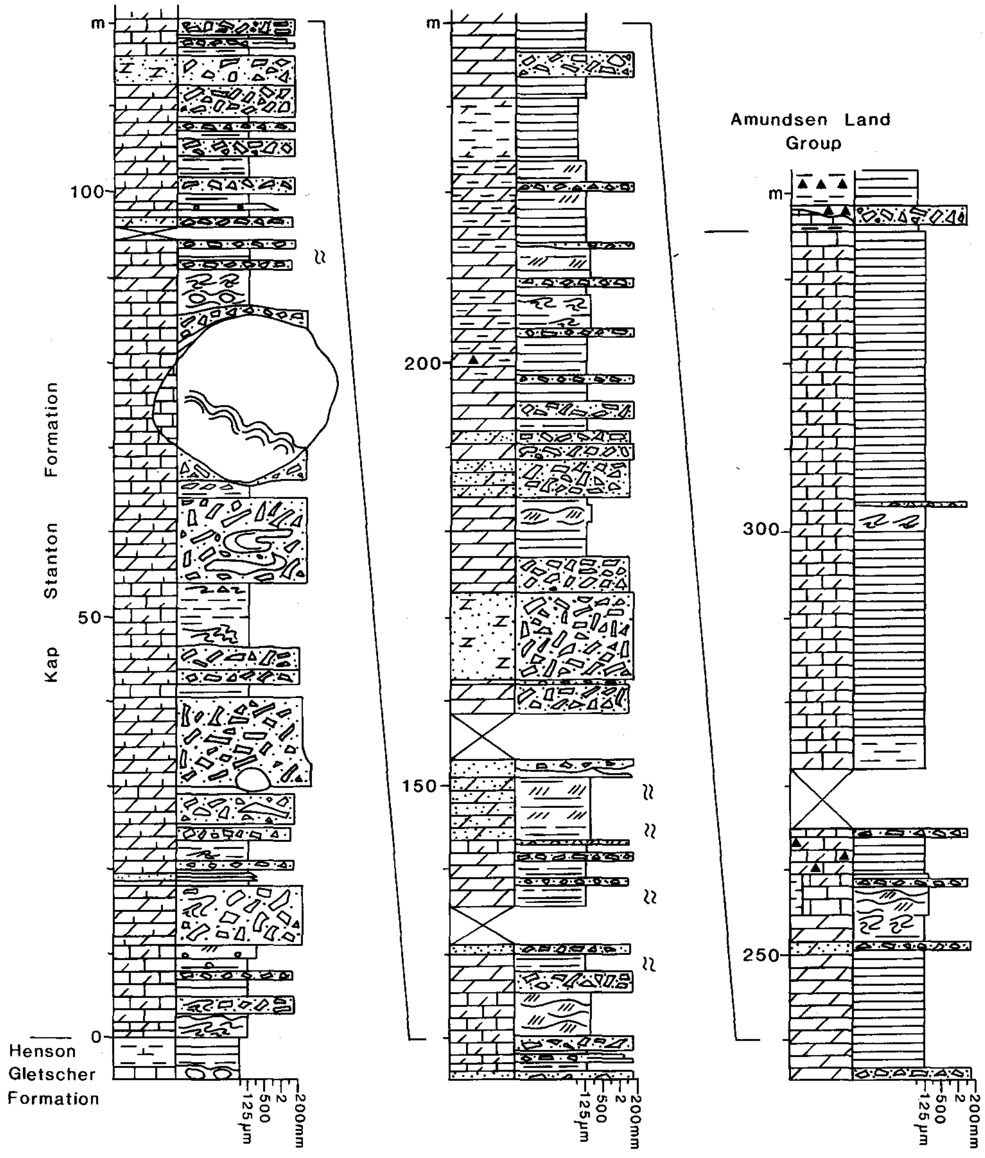


Fig. 8. Type section of the Kap Stanton Formation, northern Nyeboe Land (see Fig. 7). Note the overall decrease in thickness and abundance of carbonate breccia beds up-section.

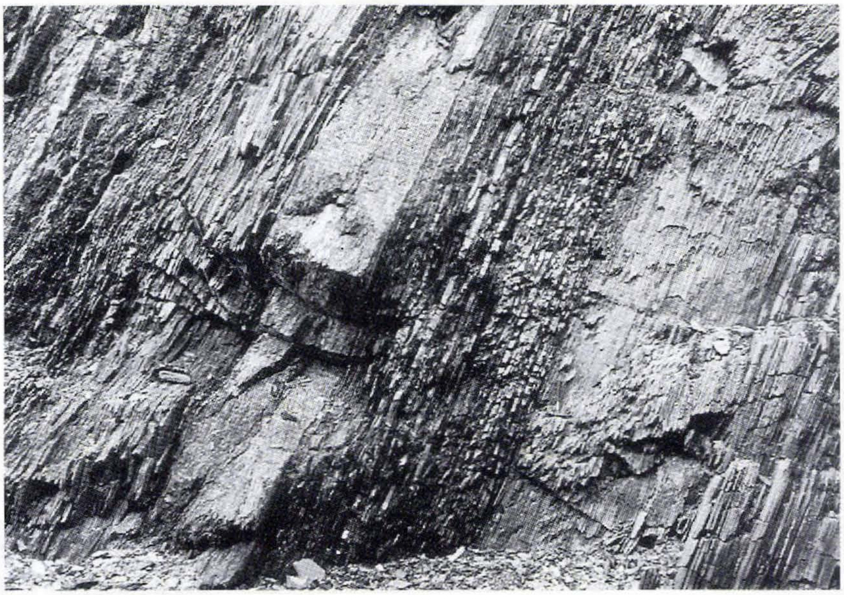


Fig. 9. Overturned thinly-bedded argillaceous lime mudstones; Kap Stanton Formation, type section (*c.* 250 m above base), northern Nyeboe Land. Massive slump-breccia bed (centre left) is about 1 m thick.

Name. After Kap Stanton, a prominent cape in northern Nyeboe Land (Fig. 7).

Type section. The type section (Fig. 8) is located *c.* 2 km west of Hand Bugt on the north coast of Nyeboe Land (Figs 1, 7). The steeply dipping, overturned strata are exposed on the east side of a small stream gully on the ridge overlooking the west shore of Hand Bugt. This is locality 1 of Babcock (1994a, b) and Robison (1994).

Thickness. The formation is about 350 m thick at the type section. It varies in thickness from c. 100 m in northern Wulff Land and Lauge Koch Land to nearly 200 m at J. P. Koch Fjord and over 300 m in Nyeboe Land.

Lithology. This prominent carbonate-rich, yellow or yellow-brown weathering formation contrasts strongly with the black or dark grey mudstones, cherts and shaly carbonates of the Henson Gletscher Formation beneath and the Amundsen Land Group above (Fig. 6b). The Kap Stanton Formation is dominated by dark grey or black argillaceous dolomites or limestones. The proportion of siliciclastic mud to carbonate mud is variable both vertically and laterally in the formation. The dark carbonate-rich mudstones typically show parallel lamination but in some sections laminated carbonates alternate with paler, burrowed carbonate mudstones producing a distinctive banded structure on a decimetre to metre scale.

At the type locality (Fig. 7), the formation is carbonate-rich relative to eastern outcrops and consists of thin, nodular or parallel-bedded argillaceous lime mudstones and dolomites interbedded with clast-supported carbonate breccia beds and thin graded skeletal-peloidal packstone or grainstone beds (Figs 8–11). Medium-grained to fine-grained, well-rounded quartz sand forms an important component in the middle of the type section (Fig. 8, 113–192 m), occurring both as discrete sandstone turbidites and as matrix in breccia beds. The nodular carbonates commonly display slope creep deformation structures such as pull-aparts, brittle slumps and interstratal breccia lenses and bands (Fig. 11). Partially dolomitised argillaceous nodular carbonates often weather to a striking orange-dark grey banding – the 'tiger limestones' of Dawes (1976). The clast composition of the mass flow breccia beds (Fig. 10) is closely comparable to the associated *in situ* nodular and thin-bedded lime mudstones suggesting derivation from the outer shelf, off-platform region. However, the type section of the Kap Stanton Formation also includes a large (*c.* 20 m diameter) platform-derived olistolith of light grey stromatolitic limestone (Fig. 8).

Farther east, the succession is less varied, being composed largely of dark grey to black argillaceous carbonate mudstones or marlstones, interbedded with rare units of ripple cross-laminated peloidal grainstone/packstone and prominent carbonate breccia beds, typically up to 10 m thick. The mass-flow breccia beds are commonly more varied in composition than those at the type section, often containing quartz sand and equidimensional metre-sized blocks of light-coloured carbonate of probable platform origin in addition to the dominant nodular or platy lime mudstone clasts. A prominent and laterally persistent breccia bed occurs near the top of the formation in the Navarana Fjord to outer J. P. Koch Fjord area (Fig. 5a).

Boundaries. The Kap Stanton Formation lies conformably between the dark mudstones, cherts and carbonates of the Henson Gletscher Formation beneath and the Amundsen Land Group above (Figs 5, 6b). The base is placed where thin-bedded or nodular argillaceous carbonate mudstones overlie recessive-weathering, shaly black mudstones and cherts with subordinate lime mudstones. In places (e.g. north Lauge Koch Land), the basal bed of the formation is a thick carbonate breccia bed.

The top is placed where prominent-weathering argillaceous platy carbonates (or marlstones) are succeeded by black cherts and shaly mudstones assigned to the Amundsen Land Group.

Distribution. The Kap Stanton Formation crops out in thrust slices and anticlinal fold closures near the north coast of North Greenland from north-west Peary Land in the east to northern Nyeboe Land in the west (Fig. 1).

Fauna and age. The boundaries of the Kap Stanton Formation are demonstrably diachronous (Fig. 4); the formation has a maximum proven age range of medial Middle Cambrian to early Ordovician. Although fossils have not been collected in the type section, rich trilobite faunas are known from the lower beds in nearby sections in northern Nyeboe Land (locality 2 in fig. 1 of Babcock, 1994a, b and Robison, 1994; see Higgins *et al.*, 1992). Associated with trilobites in these collections are bradoriids, inarticulate brachiopods and conodontomorphs. The trilobite faunas indicate a medial Middle Cambrian (*Ptychagnostus atavus* Zone) age for the basal strata in this area, as is also indicated by the uppermost collections from the Henson Gletscher Formation at the type locality of the Kap Stanton Formation (see discussion above, Babcock, 1994a, b and Robison, 1994). To the east of outer J. P. Koch Fjord, however, the lower strata of the formation are of probable late Middle Cambrian age; rich trilobite faunas indicative of the *Lejopyge laevigata* Zone of the latest Middle Cambrian were collected from *c.* 20 m above the base of the Kap Stanton Formation (see Babcock, 1994a, b; Robison, 1994) where they are associated with siliceous sponge spicules.

Much of the middle Kap Stanton Formation is unfossiliferous but shaly black argillaceous carbonates and marlstones towards the top of the formation yield graptolites of Ordovician age (Bjerreskov, 1989; Smith & Bjerreskov, 1994). West of Navarana Fjord, the uppermost beds of the formation contain Llanvirn graptolites (Bjerreskov *in* Higgins *et al.*, 1992). In other sections, however, such as in north-eastern Nyeboe Land and easternmost outcrops, graptolites from the overlying Amundsen Land Group indicate a late Tremadoc age for the top of the Kap Stanton Formation. Higgins *et al.* (1992) suggested that the Kap Stanton Formation may extend up into the late Ordovician in north-west Nyeboe Land.

Facies and depositional environment. The Kap Stanton Formation is laterally more varied than the underlying formations and records deposition in a variety of outer shelf environments. In the type area (Figs 7, 8), nodular or parallel thin-bedded, variably dolomitised argillaceous limestones dominate the formation; they typically show parallel lamination but are locally bioturbated. This facies primarily represents hemipelagic suspension deposits but probably also includes lime mud turbidites. Pull-aparts, inter-stratal brecciation and brittle slump folds testify to

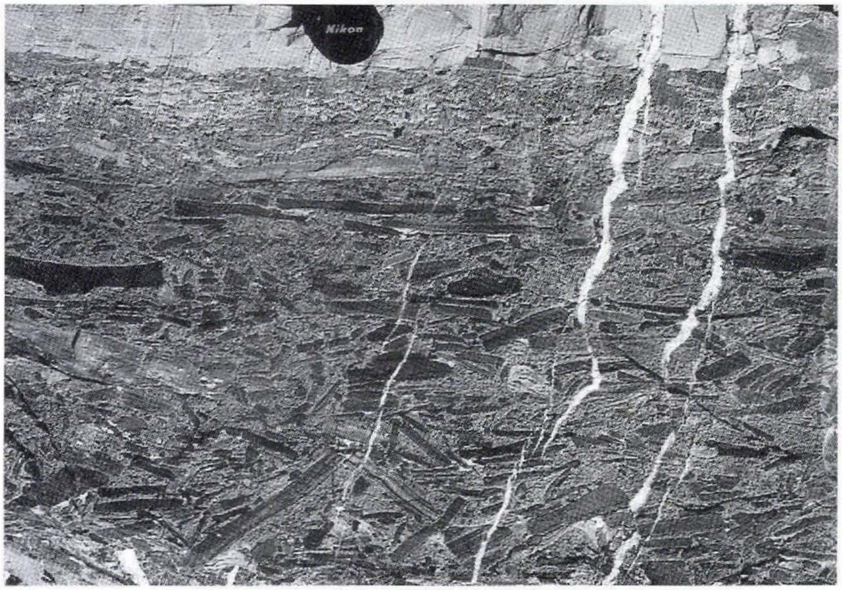


Fig. 10. Clast-supported limestone breccia bed composed of angular platy lime mudstone clasts in a lime grainstone matrix. Note the coarse-tail grading and bedding-parallel orientation of elongate clasts in the upper half of the bed. Kap Stanton Formation, type section (*c.* 100 m above base), northern Nyeboe Land.

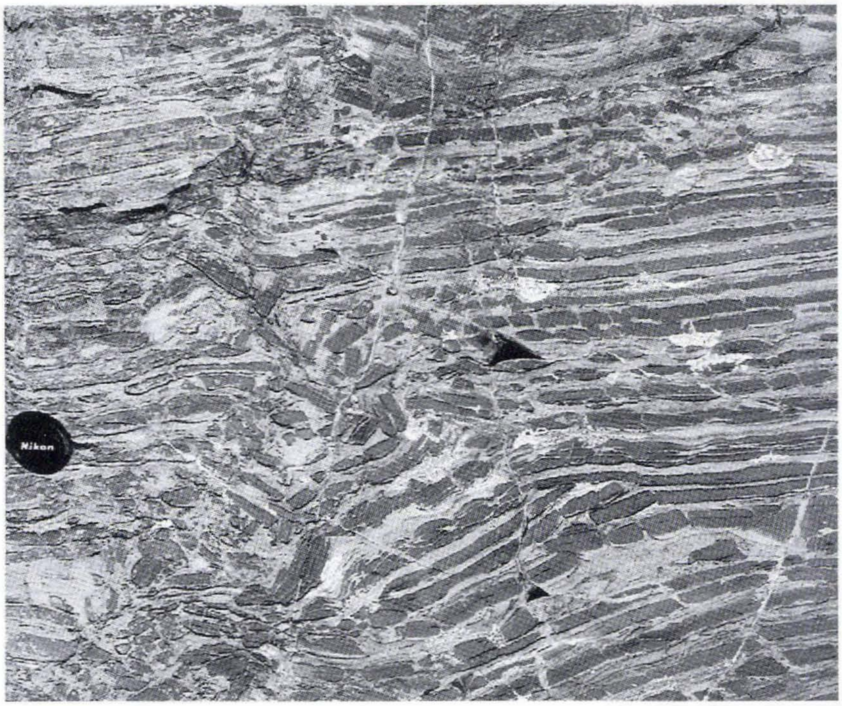


Fig. 11. Platy nodular argillaceous lime mudstones, partially dolomitised. Note the pull-aparts and brittle slump folds of inferred slope creep origin. Kap Stanton Formation, type section (*c.* 50 m above base), northern Nyeboe Land.

accumulation on a depositional slope. Graded, ripple cross-laminated packstones and grainstones, graded sandy breccias and muddy carbonate breccia beds record deposition from a range of sediment gravity flow processes. Breccia clasts are largely of off-platform origin but also include blocks derived from the coeval platform margin.

The Kap Stanton Formation in northern Nyeboe Land thus records deposition in a sub-wavebase, low-energy setting that typically received carbonate sediment in the form of hemipelagic suspension deposits, turbidites and mass-flow deposits. Evidence of a depositional slope is common and the overall setting is interpreted as a carbonate slope apron, deposited seaward of the shallow-water carbonate platform.

In eastern sections (Fig. 5a), variably dolomitised dark marlstones and argillaceous limestones dominate the formation; these become graptolitic in the upper part and primarily record deposition of clay-sized and silt-sized carbonate and siliciclastic sediment from suspension. Although typically parallel-laminated, local intervals show a distinctive rhythmic alternation of laminated and weakly bioturbated beds on a scale of 10–100 cm. Rare units of cross-laminated peloidal grainstone and packstone were deposited from tractional bottom currents; unpublished palaeocurrent data indicate shelf-parallel currents. The Kap Stanton Formation in its eastern outcrop, therefore, records deposition in a low-energy, poorly oxygenated deep shelf setting; the low carbonate content relative to the Nyeboe Land section indicates a more distal, outermost shelf environment, beyond or at the limit of carbonate dispersal from the shallow-water platform.

Palaeogeography and platform evolution

The northern outcrop of the Brønlund Fjord and Tavsens Iskappe Groups provides an extra dimension to the reconstruction of Cambrian palaeogeography in North Greenland. The southern outcrop belt documents the transition from shallow-water platform through platform margin and foreslope to carbonate slope apron and proximal outer shelf settings (Ineson, 1985, 1988; Higgins *et al.*, 1991a). The data presented here and by Higgins *et al.* (1992) allow northward extension of this palaeogeographic transect from the distal slope apron to the deep outermost shelf. A condensed succession of black shaly mudstones and cherts with rare carbonate debris beds was recorded from thrust slices along the northern coastline of North Greenland (Higgins *et al.*, 1992); these strata may extend the transect to the shelf edge or the upper basin slope.

The Brønlund Fjord and Tavsens Iskappe Groups in the northern outcrop belt record an oblique section across the outer shelf. The more proximal sections relative to the shallow-water platform occur in the west, in Nyeboe Land (Figs 1, 5b). Here the succession is nearly 500 m thick and is carbonate-dominated with sandstone interca-

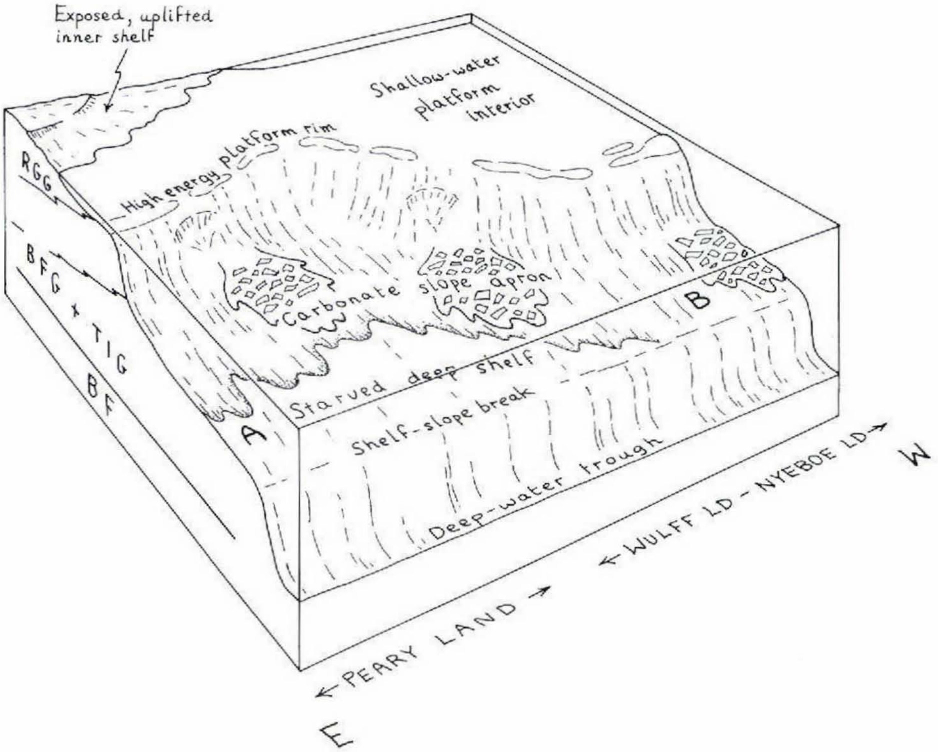


Fig. 12. Schematic block diagram showing the inferred late Middle Cambrian palaeogeography in western and central North Greenland (view from north). A and B indicate the locations of the sections in Fig. 5a, b, respectively. BF, Buen Formation; BFG, Brønlund Fjord Group; TIG, Tavsens Iskappe Group; RGG, Ryder Gletscher Group.

lations at a number of levels. The abundance of coarse-grained sediment gravity flow deposits and evidence of slope creep processes, particularly in the Kap Stanton Formation, indicate deposition in a slope apron setting. In the east, in contrast, the succession is typically 200–350 m thick and is clay-rich with only rare, thin sandstone intercalations (Fig. 5a); a distal outer shelf setting is indicated, generally beyond the range of coarse-grained sediment gravity flows derived from the upper slope apron and the platform margin to the south. Figure 12 is a schematic representation of the palaeogeography during the late Middle Cambrian showing the inferred location of the sections at Hand Bugt in the west (Fig. 5b) and outer J. P. Koch Fjord in the east (Fig. 5a).

In the J. P. Koch Fjord area, both the shelf edge and the platform margin can be accurately located (see e.g. Fig. 3). In the late Middle Cambrian, for example, the outer shelf was 70–80 km wide; the shelf edge lay about 20–30 km north of the outer J. P. Koch Fjord section (Figs 1, 5a) whilst the prograding platform margin was situated at the head of J. P. Koch Fjord, approximately 50 km south of the section (see Fig. 12). The palaeogeography of the western area is less well-constrained since neither the platform margin nor the shelf edge can be recognised; the former is covered by younger strata and the latter is inferred to lie north of the present coastline (Figs 1, 3). The evolution of the platform can be inferred, however, by analogy with the eastern succession.

Despite the lateral variation in thickness and facies from east to west, the overall stratigraphy of the northern outcrop is remarkably uniform, suggesting that platform evolution in the west followed a similar pattern to that recorded in the east (Ineson, 1985, 1988; Ineson & Peel, 1987; Higgins *et al.*, 1991a). Indeed, the Aftenstjernesø and Henson Gletscher Formations at Hand Bugt in northern Nyeboe Land (Figs 1, 5b) are comparable both in thickness and overall facies development to the type sections of these formations at the head of J. P. Koch Fjord, some 250 km to the east (see fig. 22 in Ineson, 1980; Ineson & Peel, unpublished). This suggests that these uppermost Lower–Middle Cambrian sediments at Hand Bugt were deposited some 10–20 km north of the platform margin, which was probably a progradational, depositional margin (*sensu* McIlreath & James, 1979) at this time, as observed in the east (Ineson 1985, 1988; Ineson & Peel, 1987).

The Kap Stanton Formation at Hand Bugt, Nyeboe Land can be subdivided into three discrete intervals that record discrete phases or events in platform evolution. The lower unit (Fig. 8, 0–113 m) is carbonate-dominated and includes abundant, thick carbonate debris sheets and turbidites; this interval records a period of extensive shedding of fine-grained sediment from the coeval platform and progradation of the slope apron by sliding and resedimentation of peri-platform fines. This style of sedimentation is well-known from eastern outcrops where it can be correlated with periods of platform progradation (Ineson & Peel, 1987; Ineson, 1988; Higgins *et al.*, 1991a). It can be suggested, therefore, that during the late Middle to Late Cambrian, the western platform continued to prograde northwards, possibly extending as far north as the Navarana Fjord lineament (Fig. 1).

The middle unit of the Kap Stanton Formation at Hand Bugt (Fig. 8, 113–192 m) is characterised by the appearance of medium-grained to fine-grained, well-rounded quartz sand, occurring both as discrete sandstone turbidites and as matrix in thick sandstone-dolomite debris beds. Such facies have been recorded from approximately the same level in most sections through the formation (Fig. 5a, 180 m, 220 m; Higgins *et al.*, 1992). It is probable that this incursion of siliciclastic sand onto the outer shelf was related to the northward and westward progradation of quartz sands during the Late Cambrian and earliest Ordovician associated with the culmination of uplift of the eastern shelf (Surlyk & Hurst, 1984; Surlyk, 1991). In western Peary Land and Freuchen Land, the Perssuaq Gletscher Formation records the northward progradation of sandstones into the outer shelf environment (Surlyk & Ineson, 1987) whereas the Permin Land Formation, and the correlative Kap Coppinger Member of the Cass Fjord Formation, record the westward extension of these sands across the shallow-water platform of western North Greenland (Bryant & Smith, 1990). The eastern shelf was largely exposed at this time (see Figs 2, 12), and siliciclastic sand bypassed the shelf to form the basinal sandstone turbidites of the Vølvedal Group, in Johannes V. Jensen Land (Surlyk & Hurst, 1984; Higgins *et al.*, 1991a). The sandstones of the Kap Stanton Formation thus mark a significant stage in the evolution of the shelf when much of the eastern portion of the platform was exposed and thus producing little carbonate sediment. Sedimentation on the carbonate platform in the west was apparently continuous but productivity was probably reduced due to the siliciclastic influx, resulting in a decrease in the export of carbonate sediment to the deep shelf and a slowing or cessation of platform progradation.

The upper 150 m of the Kap Stanton Formation in the type section (Fig. 8) show an upward decrease in the proportion of carbonate mudstone relative to siliciclastic mudstone, and an overall decrease in both thickness and abundance of coarser resedimented carbonate deposits. This overall upward decrease in the proportion of carbonate is a feature of the Kap Stanton Formation throughout its outcrop (see Fig. 5 and Higgins *et al.*, 1992) and reflects a general decrease with time in the carbonate export potential of the shallow-water platform. This may have resulted from decreased productivity of the platform but the preservation of a thick Cambro-Ordovician carbonate platform succession in central and western North Greenland (Higgins *et al.*, 1991a) makes it more likely that the decrease records a shift in the style of platform growth. The nature of the latest Cambrian – Early Ordovician platform margin is unknown since it is nowhere exposed in North Greenland. It is clear from the Cambrian and Middle Ordovician – Lower Silurian record of platform evolution, however, that this period marked a shift from a progradational style during the Cambrian to an aggradational style during the latter part of the Ordovician and the Early Silurian, when the platform margin was anchored by differential subsidence across the Navarana Fjord lineament (Hurst & Surlyk, 1983; Surlyk & Hurst, 1984; Higgins *et al.*, 1991a; Surlyk & Ineson, 1992).

The gradual upward decrease in carbonate in the uppermost Cambrian to Lower Ordovician strata of the Kap Stanton Formation probably records this shift in platform margin development from progradational to aggradational, possibly initiated by the onset of differential subsidence along the Navarana Fjord lineament in the latest Cambrian.

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References

Babcock, L. E. 1994a: Polymeroid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Bull. Grønlands geol. Unders.* **169** (this volume).

Babcock, L. E. 1994b: Biogeography and biofacies patterns of Middle Cambrian polymeroid trilobites from North Greenland: palaeogeographic and palaeo-oceanographic implications. *Bull. Grønlands geol. Unders.* **169** (this volume).

Blaker, M. R. 1991: Early Cambrian trilobites from North Greenland. Unpublished Ph.D. thesis, Keele Univ., 286 pp.

Bendix-Almgreen, S. E. & Peel, J. S. 1988: *Hadimopanella* from the Lower Cambrian of North Greenland: structure and affinities. *Bull. geol. Soc. Denmark* **37,** 83–103.

Bjerreskov, M. 1989: Ordovician graptolite biostratigraphy in North Greenland. *Rapp. Grønlands geol. Unders.* **144,** 17–33.

Bryant, I. D. & Smith, M. P. 1990: A composite tectonic-eustatic origin for shelf sandstones at the Cambrian–Ordovician boundary in North Greenland. *J. geol. Soc. Lond.* **147,** 795–809.

Christiansen, F. G., Nøhr-Hansen, H. & Nykjær, O. 1987: The Cambrian Henson Gletscher Formation: a mature to post-mature hydrocarbon source rock sequence from North Greenland. *Rapp. Grønlands geol. Unders.* **133**, 141–157.

Dawes, P. R. 1976: Precambrian to Tertiary of northern Greenland. *In* Watt, W. S. & Escher, A. (ed.) *Geology of Greenland*, 248–303. Copenhagen: Geol. Surv. Greenland.

Dawes, P. R. & Peel, J. S. 1984: Biostratigraphic reconnaissance in the Lower Palaeozoic of western North Greenland. *Rapp. Grønlands geol. Unders.* **121**, 19–51.

Friderichsen, J. D., Higgins, A. K., Hurst, J. M., Pedersen, S. A. S., Soper, N. J. & Surlyk, F. 1982: Lithostratigraphic framework of the Upper Proterozoic and Lower Palaeozoic deep water clastic deposits of North Greenland. *Rapp. Grønlands geol. Unders.* **107**, 20 pp.

Frykman, P. 1980: A sedimentological investigation of the carbonates at the base of the Brønlund Fjord Group (Early–Middle Cambrian), Peary Land, eastern North Greenland. *Rapp. Grønlands geol. Unders.* **99**, 51–55.

Håkansson, E., Heinberg, C. & Stemmerik, L. 1991: Mesozoic and Cenozoic history of the Wandel Sea Basin area, North Greenland. *Bull. Grønlands geol. Unders.* **160**, 153–164.

Higgins, A. K. & Soper, N. J. 1985: Cambrian – Lower Silurian slope and basin stratigraphy between northern Nyeboe Land and western Amundsen Land, North Greenland. *Rapp. Grønlands geol. Unders.* **126**, 79–86.

Higgins, A. K., Soper, N. J. & Friderichsen, J. D. 1985: North Greenland fold belt in eastern North Greenland. *In* Gee, D. G. & Sturt, B. A. (ed.) *The Caledonide orogen – Scandinavia and related areas*, 1017–1029. London: John Wiley & Son Ltd.

Higgins, A. K., Ineson, J. R., Peel, J. S., Surlyk, F. & Sønderholm, M. 1991a: Lower Palaeozoic Franklinian Basin of North Greenland. *Bull. Grønlands geol. Unders.* **160,** 71–139.

Higgins, A. K., Ineson, J. R., Peel, J. S., Surlyk, F. & Sønderholm, M. 1991b [issued 1992]: Cambrian to Silurian basin development and sedimentation, North Greenland. *In* Trettin, H. P. (ed.) Geology of the Innuitian orogen and arctic platform of Canada and Greenland, 111–161. *Geology of Canada* **3**. (Also *The geology of North America* **E.**) Ottawa: Geological Survey of Canada.

Higgins, A. K., Soper, N. J. & Davis, N. C. 1992: Lower Palaeozoic outer shelf and slope lithostratigraphy, Franklinian basin, North Greenland. *Open File Ser. Grønlands geol. Unders.* **92/8,** 57 pp.

Hurst, J. M. & Surlyk, F. 1983: Initiation, evolution and destruction of an early Paleozoic carbonate shelf, eastern North Greenland. *J. Geol.* **91**, 671–691.

Ineson, J. R. 1980: Carbonate debris flows in the Cambrian of south-west Peary Land, eastern North Greenland. *Rapp. Grønlands geol Unders.* **99**, 43–49.

Ineson, J. R. 1985: The stratigraphy and sedimentology of the Brønlund Fjord and Tavsens Iskappe Groups (Cambrian) of Peary Land, eastern North Greenland. Unpublished Ph.D. thesis, Keele Univ., 310 pp.

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

Ineson, J. R. & Peel, J. S. 1980: Cambrian stratigraphy in Peary Land, eastern North Greenland. *Rapp. Grønlands geol. Unders.* **99**, 33–42.

Ineson, J. R. & Peel, J. S. 1987: Cambrian platform-outer shelf relationships in the Nordenskiöld Fjord region, central North Greenland. *Rapp. Grønlands geol. Unders.* **133**, 13–26.

Ineson, J. R. & Peel, J. S. unpublished: Cambrian shelf stratigraphy of the Peary Land region, central North Greenland. Manuscript for Grønlands Geologiske Undersøgelse.

McIlreath, I. A. & James, N. P. 1979: Carbonate slopes. *In* Walker, R. G. (ed.) *Facies models*, 113–143. Geoscience Canada.

Palmer, A. R. & Peel, J. S. 1979: New Cambrian faunas from Peary Land, eastern North Greenland. *Rapp. Grønlands geol. Unders.* **91**, 29–36.

Peel, J. S. 1974: Lower Cambrian fossils from Nyeboe Land, North Greenland fold belt. *Rapp. Grønlands geol. Unders.* **65,** 17 only.

Peel, J. S. 1979a: Cambrian – Middle Ordovician stratigraphy of the Adams Gletscher region, south-west Peary Land, North Greenland. *Rapp. Grønlands geol. Unders.* **88,** 29–39.

Peel, J. S. 1979b: *Serrodiscus* from northern Nyeboe Land, North Greenland. *Rapp. Grønlands geol. Unders.* **91,** 116 only.

Peel, J. S. 1994: An enigmatic cap-shaped fossil from the Middle Cambrian of North Greenland. *Bull. Grønlands geol. Unders.* **169** (this volume).

Peel, J. S. & Larsen, N. H. 1984: *Hadimopanella apicata* from the Lower Cambrian of western North Greenland. *Rapp. Grønlands geol. Unders.* **121**, 89–96.

Peel, J. S., Conway Morris, S. & Ineson, J. R. 1992: A second glimpse of Early Cambrian life: new collections from Sirius Passet, North Greenland. *Rapp. Grønlands geol. Unders.* **155,** 48–50.

Resser, C. E. 1939: The *Ptarmigania* strata of the northern Wasatch Mountains. *Smithson. Misc. Collns* **98**(24), 72 pp.

Robison, R. A. 1994: Agnostoid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Bull. Grønlands geol. Unders.* **169** (this volume).

Smith, M. P. & Bjerreskov, M. 1994: The Ordovician System in Greenland. *Int. Union geol. Sci. Publ.* **29A**, 1–46.

Soper, N. J. & Higgins, A. K. 1990: Models for the Ellesmerian mountain front in North Greenland: a basin margin inverted by basement uplift. *J. struct. Geol.* **12**, 83–97.

Stemmerik, L. & Håkansson, E. 1991: Carboniferous and Permian history of the Wandel Sea Basin, North Greenland. *Bull. Grønlands geol. Unders.* **160**, 141–151.

Surlyk, F. 1991: Tectonostratigraphy of North Greenland. *Bull. Grønlands geol. Unders.* **160**, 25–47.

Surlyk, F. & Hurst, J. M. 1983: Evolution of the early Paleozoic deep-water basin of North Greenland – aulacogen or narrow ocean? *Geology* **11**, 77–81.

Surlyk, F. & Hurst, J. M. 1984: The evolution of the early Paleozoic deep-water basin of North Greenland. *Bull. geol. Soc. Am.* **95**, 131–154.

Surlyk, F. & Ineson, J. R. 1987: Aspects of Franklinian shelf, slope and trough evolution and stratigraphy in North Greenland. *Rapp. Grønlands geol. Unders.* **133**, 41–58.

Surlyk, F. & Ineson, J. R. 1992: Carbonate gravity flow deposition along a platform margin scarp (Silurian, North Greenland. *J. sed. Petrol.* **62**, 400–410.

Agnostoid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland

Richard A. Robison

Agnostoid trilobites are abundant and diverse in 10 collections from the Henson Gletscher and Kap Stanton formations of North Greenland. Three agnostoid assemblages are identified from slope apron to deep outer shelf lithofacies, representing the *Ptychagnostus gibbus, Ptychagnostus atavus,* and lower *Lejopyge laevigata* interval-zones of Middle Cambrian age. This is the first report of fossils from the *P. atavus* Zone in Greenland.

At least 17 agnostoid genera are represented in the Henson Gletscher and Kap Stanton formations, of which *Megagnostus* and *Schismagnostus* are new. Diagnoses of *Agnostus, Diplorrhina, Doryagnostus, Lejopyge, Peratagnostus, Peronopsis, Pseudophalacroma*, and *Tomagnostus* are emended. From review of type material, some of which is illustrated with new photographs, *Cyclopagnostus, Grandagnostus, Phoidagnostus, Quadragnostus*, and *Spinagnostus* are considered to be unrecognisable genera.

Forty agnostoid species, some in open nomenclature, are identified from the new collections. The species *Agnostus lophotus, Diplorrhina oncota, Megagnostus diclidus, Schismagnostus plicatus*, and *Tomagnostus bothrus* are new. Abrupt early holaspid metamorphosis occurred in the cephalon of *Schismagnostus plicatus* and in the pygidium of *Peratagnostus cicer*. A lectotype is selected for *Agnostus lens* Grönwall, 1902, which is the type species of *Cotalagnostus*.

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The geological setting, lithostratigraphy, and depositional environments of the Henson Gletscher and Kap Stanton formations are discussed in an accompanying paper by Ineson *et al.* (1994). These formations represent deposition in slope apron to deep outer shelf environments, and they contain rich Middle Cambrian faunas dominated by trilobite assemblages that are unusual in having Laurentian, Baltic, and mixed aspects. Systematic descriptions of the trilobites and discussions of their biostratigraphy are presented in separate papers, one on the polymeroids by Babcock (1994a), and one here on the agnostoids. Separate biostratigraphic zonations for agnostoid and polymeroid trilobites have been advocated because of major differences in their morphology, distributions, and inferred modes of life (e.g., Robison, 1976, 1984). The agnostoids were probably pelagic suspension feeders whereas most polymeroids were probably benthic deposit feeders (e.g., Robison, 1972b, 1987).

Molluscs, brachiopods, ostracods, and sponges are present in the studied collections from the Henson Gletscher and Kap Stanton formations, but they have not been studied in detail.

Analyses of selected Middle Cambrian trilobite faunas and their depositional environments suggest that differences between faunas of Laurentian and Baltic aspect are related to environmental gradients in which temperature was a major factor. This hypothesis is evaluated in another accompanying paper by Babcock (1994b), which discusses palaeogeography and trilobite biogeography.

This paper is based on diverse agnostoid trilobites (Table 1) in 10 collections from North Greenland. The fossils were collected at two localities in Nyeboe Land and at one locality in Peary Land (Fig. 1) by John S. Peel and other geologists of the Geological Survey of Greenland (GGU) during regional geological investigations.

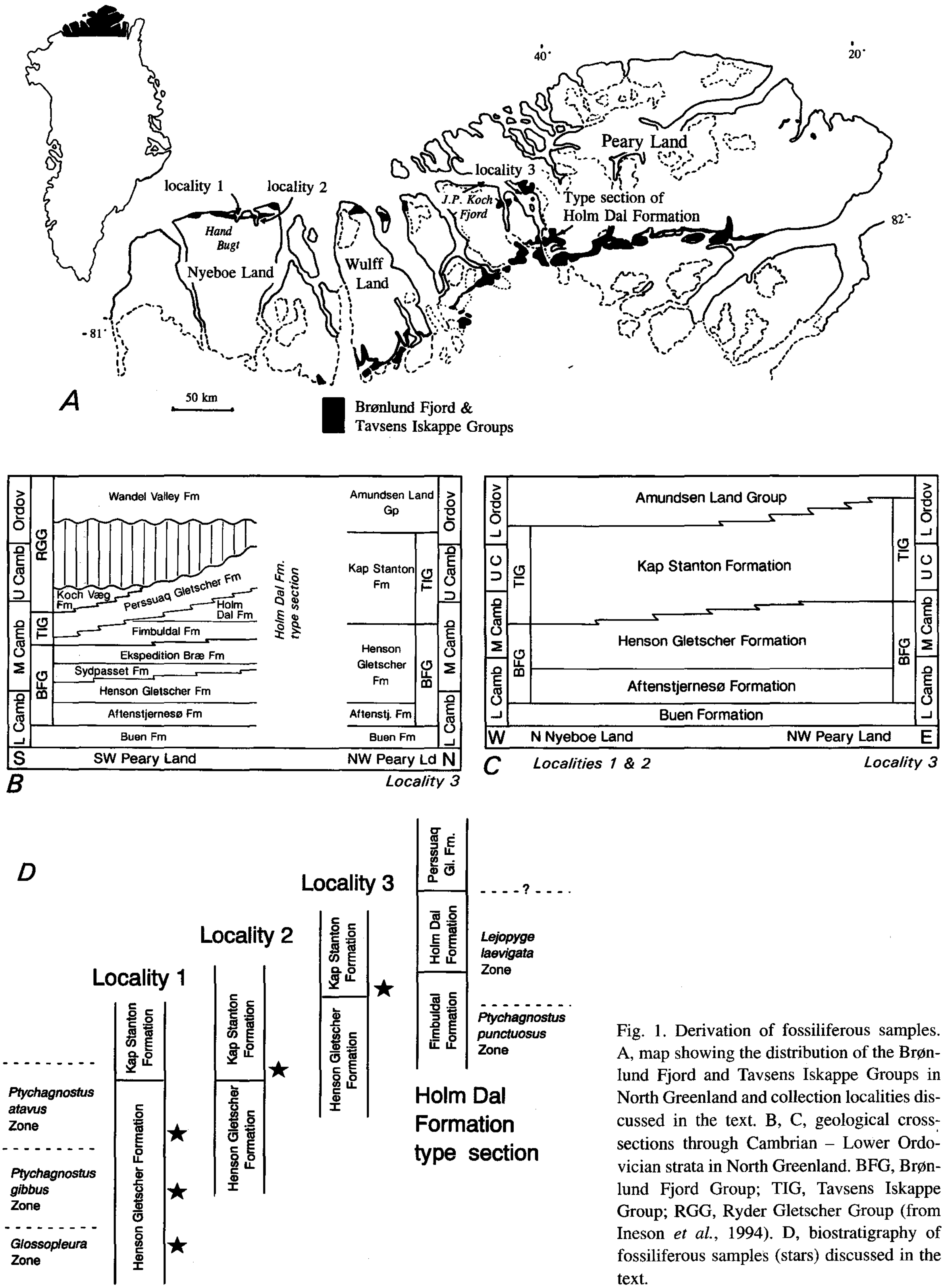

Fig. 1. Derivation of fossiliferous samples. A, map showing the distribution of the Brønlund Fjord and Tavsens Iskappe Groups in North Greenland and collection localities discussed in the text. B, C, geological cross-sections through Cambrian – Lower Ordovician strata in North Greenland. BFG, Brønlund Fjord Group; TIG, Tavsens Iskappe Group; RGG, Ryder Gletscher Group (from Ineson *et al.*, 1994). D, biostratigraphy of fossiliferous samples (stars) discussed in the text.

Biostratigraphy

Five agnostoid interval-zones have been defined in Middle Cambrian strata (Robison, 1984, pp. 5–9). With the aid of both defining and characterising species (*sensu* Murphy, 1977), these zones are identifiable in many open-marine lithofacies of the world. Three of the zones, *Ptychagnostus gibbus*, *Ptychagnostus atavus*, and *Lejopyge laevigata*, are represented by rich and diverse agnostoid assemblages in the new GGU collections from North Greenland. Lack of fossils from the *Ptychagnostus praecurrens* and *Ptychagnostus punctuosus* zones is probably due to incomplete collecting, in part because of such problems as ground accessibility and limited field time (J. S. Peel, personal communication, 1987), rather than to gaps in the stratigraphic succession. Previous reports of trilobites from the *P. punctuosus* Zone in Nyeboe Land (Poulsen, 1969) and Peary Land (Robison, 1984) support this conclusion.

Ptychagnostus gibbus Interval-zone

One collection (GGU 298970) from the middle Henson Gletscher Formation of Nyeboe Land contains 12 species-group taxa (Fig. 2), including *P. gibbus*. More than half of these species are widely distributed around the world, and collectively the assemblage is most characteristic of the *gibbus* Zone. Other evidence supporting this zonal identification is the presence of *Ptychagnostus intermedius,* a common and cosmopolitan species with an observed stratigraphic range that is restricted to the *gibbus* Zone. Observed ranges of other species, especially that of *Doryagnostus vinicensis,* as revised, suggest that the collection is from the upper part of the *gibbus* Zone.

Ptychagnostus atavus Interval-zone

The *atavus* Zone is well represented by abundant specimens in five collections, all from Nyeboe Land. Of these collections, three (GGU 298969, 298974, 298975) are from the upper Henson Gletscher Formation (Fig. 2) and two (GGU 319789, 319790) are from basal beds of the Kap Stanton Formation (Fig. 3). The total zonal assemblage contains at least 24 species-group taxa, including *P. atavus*. Although fossils of this zone are widely distributed (Rowell *et al.*, 1982), this is the first report of diagnostic species in Greenland (cf. Robison, 1984, p. 7). The presence of *Ptychagnostus affinis* in basal beds of the Kap Stanton Formation suggests that those beds are in the upper *atavus* Zone, possibly near its boundary with the *Ptychagnostus punctuosus* Zone.

Table 1. Classification of agnostoid trilobites identified from the Henson Gletscher and Kap Stanton formations

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- Order Agnostida
  - Family Agnostidae
    - *Agnostus lophotus* n. sp.
    - *Agnostus*? cf. *exsulatus* Poulsen
  - Family Clavagnostidae
    - *Clavagnostus* cf. *milli* Jago & Daily
  - Family Diplagnostidae
    - *Diplagnostus planicauda* (Angelin)
    - *Iniospheniscus incanus*? Öpik
    - *Linguagnostus groenwalli* Kobayashi
  - Family Doryagnostidae
    - *Doryagnostus vinicensis* (Šnajdr)
  - Family Metagnostidae
    - *Diplorrhina oncota* n. sp.
    - *Diplorrhina* cf. *sallesi* (Munier-Chalmas & Bergeron)
  - Family Peronopsidae
    - *Hypagnostus brevifrons* (Angelin)
    - *Hypagnostus parvifrons* (Linnarsson)
    - *Peronopsis bulkurensis* Pokrovskaya & Pegel
    - *Peronopsis fallax* (Linnarsson)
    - *Peronopsis ferox* (Tullberg)
    - *Peronopsis interstricta* (White)
    - *Peronopsis* cf. *pusilla* (Tullberg)
    - *Peronopsis scutalis* (Hicks)
    - *Peronopsis* sp. 1
    - *Peronopsis* sp. 2
    - *Peronopsis* sp. 3
  - Family Ptychagnostidae
    - *Lejopyge barrandei* (Hicks)
    - *Lejopyge calva* Robison
    - *Lejopyge hybridus* (Brøgger)
    - *Lejopyge* cf. *seminula* (Whitehouse)
    - *Ptychagnostus affinis* (Brøgger)
    - *Ptychagnostus atavus* (Tullberg)
    - *Ptychagnostus gibbus* (Linnarsson)
    - *Ptychagnostus intermedius* (Tullberg)
    - *Tomagnostus bothrus* n. sp.
    - *Tomagnostus corrugatus* (Illing)
    - *Tomagnostus fissus* (Linnarsson)
    - *Tomagnostus perrugatus* (Grönwall)
  - Family unassigned
    - *Megagnostus diclidus* n. gen. & n. sp.
    - *Megagnostus glandiformis* (Angelin), n. gen.
    - *Peratagnostus cicer* (Tullberg)
    - *Phalagnostus ovalis* (Illing)
    - *Schismagnostus plicatus* n. gen. & n. sp.
    - *Toragnostus bituberculatus* (Angelin)
    - Genus & species undetermined 1
    - Genus & species undetermined 2

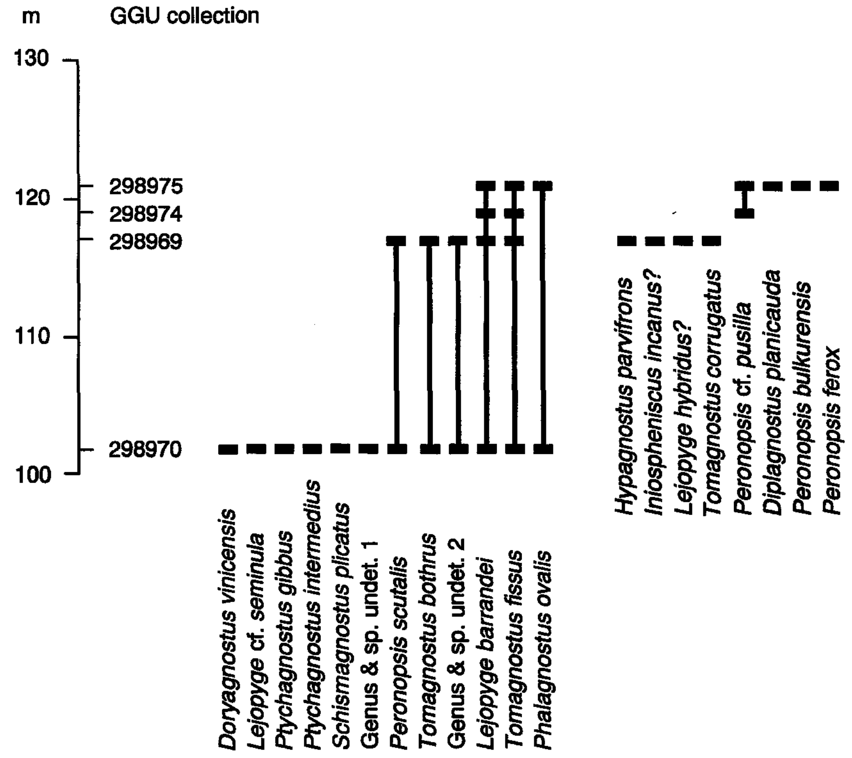


Fig. 2. Stratigraphic distribution of agnostoid species described from the upper Henson Gletscher Formation in Nyeboe Land (locality 1, Fig. 1). Scale indicates height in metres above base of formation. Six-digit numbers designate GGU collections. GGU 298970 is from the *Ptychagnostus gibbus* Zone. GGU 298969, 298974, and 298975 are from the *Ptychagnostus atavus* Zone.

Lejopyge laevigata Interval-zone

The *laevigata* Zone is represented by abundant specimens in four collections (GGU 301311–301313, 313115), all from basal beds of the Kap Stanton Formation in Peary Land (Fig. 4). At least 12 species-group taxa are represented, which collectively are characteristic of

GGU collection	319789	319790
Agnostus? cf. exsulatus	■	■
Diplorrhina cf. sallesi	■	
Hypagnostus parvifrons	■	■
Lejopyge barrandei	■	■
Linguagnostus groenwalli	■	■
Peronopsis fallax	■	■
Peronopsis interstricta	■	■
Peronopsis scutalis	■	■
Peronopsis sp. 1	■	
Phalagnostus ovalis	■	■
Ptychagnostus affinis	■	■
Tomagnostus perrugatus	■	■
Lejopyge hybridus		■
Peronopsis cf. pusilla		■
Peronopsis sp. 2		■
Ptychagnostus atavus		■

Fig. 3. Distribution of agnostoid species in GGU collections from basal beds of the Kap Stanton Formation in Nyeboe Land (locality 2, Fig. 1). Collections are not in stratigraphic sequence. Both collections are from the *Ptychagnostus atavus* Zone, and probably from its upper part.

GGU collection	301311	301312	301313	313115
Lejopyge calva	■			
Lejopyge hybridus?	■			
Agnostus lophotus		■	■	■
Clavagnostus cf. milli		■	■	■
Hypagnostus brevifrons		■	■	■
Megagnostus diclidis		■	■	■
Megagnostus glandiformis		■	■	■
Peratagnostus cicer		■	■	■
Toragnostus bituberculatus		■	■	■
Diplagnostus planicauda			■	
Diplorrhina oncota			■	■
Peronopsis sp. 3			■	

Fig. 4. Distribution of agnostoid species in GGU collections from basal beds of the Kap Stanton Formation in Peary Land (locality 3, Fig. 1). Collections are not in stratigraphic sequence. All collections are from the lower *Lejopyge laevigata* Zone.

the informal lower subzone of the *laevigata* Zone (Robison, 1984). Although *L. laevigata* is not present in these collections, the species has been described from farther south in Peary Land (Robison, 1984, 1988), where enclosing strata of the Holm Dal Formation have been interpreted to represent deposition in an outer shelf environment (Ineson, 1988).

Systematic descriptions

Terminology

Morphological terms used here are mostly defined in the *Treatise on Invertebrate Paleontology* (Harrington *et al.*, 1959). Additional terms have been defined by Robison (1964, 1982), Öpik (1967), and Shergold *et al.* (1990).

A common, iterative, evolutionary trend among agnostoid trilobites was the suppression of dorsal furrows and other surface irregularities, mostly on the acrolobes. The condition resulting from advanced suppression of such features has commonly been referred to by the adjective *effaced* (e.g., Shergold *et al.* 1990, p. 11). The opposite primitive condition, with ordinary development of lobes and furrows has no commonly used term, although it has been called 'en grande tenue' by some authors (e.g., Öpik, 1967, p. 56; Shergold *et al.*, 1990, p. 11). This latter term is not an adjective, and to simplify terminology, I here refer to the primitive agnostoid condition as *furrowed.* Unless otherwise stated, the furrowed condition is a character state of all taxa diagnosed here.

Repositories

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

Phylum Arthropoda

Class Trilobita

Order Agnostida Salter, 1864

Remarks. The diagnosis of Agnostida by Robison (1984, pp. 9–10) is followed here. The author of the taxon, however, is J. W. Salter (Shergold *et al.*, 1990, p. 4). Using recently obtained information on ventral morphology, Walossek & Müller (1990) have critically evaluated the phyletic relationships of agnostoids and stem-lineage crustaceans. A phylogenetic analysis by Babcock (1994a) suggests that the Agnostida is monophyletic.

Family Agnostidae M'Coy, 1849

Genus *Agnostus* Brongniart, 1822

Agnostus Brongniart, 1822, pp. 8, 38; Jaekel, 1909, p. 399; Kobayashi, 1939, pp. 159–162; Westergård, 1946, pp. 68–69, 84; Howell *in* Harrington *et al.,* 1959, pp. O172–O173; Pokrovskaya *in* Chernysheva, 1960, p. 58; Egorova & Pokrovskaya *in* Khalfin, 1960, pp. 159–160; Öpik, 1961, pp. 74–75; Palmer, 1962, p. F-12; Shergold *et al.*, 1990, pp. 32–33 [selected references only]

Battus Dalman, 1828, pp. 136–137

Acutatagnostus Ergaliev, 1980, p. 91

Type species. Entomostracites pisiformis Wahlenberg, 1818, p. 42; by monotypy. Authorship of the species name was reviewed by Rushton (1978, p. 258).

Emended diagnosis. Cephalon having preglabellar median furrow. Glabella unequally divided by transverse furrow (F3); anterior end rounded to ogival, posterior end rounded to acuminate. Basal lobes simple, may indent glabella. Genae smooth or weakly scrobiculate. Thorax unmodified. Pygidium axiolobate and simplimarginate. Axis separated from posterior border furrow; F1 and F2 moderately developed to nearly effaced; M2 with strong, oval to carinate, median tubercle. Pleural fields posteriorly confluent. Borders of cephalon and pygidium relatively narrow. Pygidial border having pair of small posterolateral spines. Border furrows increasing in relative width during ontogeny.

Remarks. Following its validation in 1822, more than 250 species-group taxa were assigned to *Agnostus*, including most of the agnostoids named during the nineteenth and early twentieth centuries. With erection of many agnostoid genera during the twentieth century, most species of *Agnostus* were reassigned to new genera. The progressive removal of species eventually left the genus with its type species, *A. pisiformis,* and a residue of species-group taxa that mostly lack definitive generic characters. Although the species content of *Agnostus* has significantly changed during its taxonomic history, little attention has been given to its definition and concept.

Following the reassignment of most of its species, a series of brief diagnoses of *Agnostus* were published by Kobayashi (1939, pp. 150–160), Howell (*in* Harrington *et al.*, 1959, pp. O172–O173), Pokrovskaya (*in* Chernysheva, 1960, p. 58), Egorova & Pokrovskaya (*in* Khalfin, 1960, pp. 159–160), and Palmer (1962, p. F12). Of those authors, Kobayashi was the only one to list a complement of species, and most of those were subsequently reassigned to other genera. Westergård (1946) did not give a diagnosis of *Agnostus*, but he did diagnose or discuss four species-group taxa under the generic name, including the new species *A. neglectus.* In 1967, Öpik (pp. 98–99) established the genus *Innitagnostus,* which he differentiated from *Agnostus* "and related groups (*Homagnostus, Geragnostus, Micragnostus*)" by the presence of "a laterally notched glabella with angulate recesses to fit the basal lobes." A new species, *I. innitens,* was described by Öpik as the type of *Innitagnostus,* and he also reassigned to that genus *Agnostus inexpectans* Kobayashi, 1938, *A. neglectus,* and *Tomagnostus tchatertensis* Kryskov *in* Borovikov & Kryskov, 1963. Recently, Shergold *et al.* (1990) published the most detailed diagnoses to date of both *Agnostus* and *Innitagnostus,* but without accompanying taxonomic discussion or indication of assigned species.

After reviewing the taxonomy of *Agnostus* and closely related genera, I no longer support the recognition of *Innitagnostus* as a valid genus. Henningsmoen (1958, pl. 5, figs 1–12) has well illustrated some of the variation observed within populations of *A. pisiformis,* the type species of *Agnostus*. His illustrations show that some specimens have a glabella notched to fit the basal lobes and others do not. Some specimens also have weak abaxial development of the F1 and F2 furrows, giving a 'laterally notched' aspect to the glabella, and others do not. This variation in the type species of *Agnostus* encompasses the only two characters cited by Öpik (1967, p. 98) to differentiate *Innitagnostus* from *Agnostus*. In my judgment, a more important character of *I. innitens,* the type species of *Innitagnostus,* is the near effacement of its preglabellar median furrow. This and its other characters, especially those of its axial lobe, suggest that *I. innitens* is a transitional species linking *Agnostus* and *Micragnostus* (*sensu* Fortey, 1980, pp. 21–22). Its observed stratigraphic occurrence also accords with this suggestion. Although the transitional characters of *I. innitens* make its generic assignment arbitrary, based on the near effacement of its preglabellar median furrow, I reassign it to *Micragnostus*. Consequently, *Innitagnostus* is considered to be a junior synonym of *Micragnostus*.

Among the characteristic features of *Agnostus* is a preglabellar median furrow, which normally is absent in late holaspid instars of *Micragnostus*. A vestige of the furrow, however, may be evident in younger instars of some species of *Micragnostus* (e.g., *M. intermedius;* see Robison & Pantoja-Alor 1968, pl. 97, figs 3–5, as reassigned by Fortey, 1980, p. 21).

Agnostus, as emended, includes *A. pisiformis* (Wahlenberg, 1818), *A. pater* Westergård *in* Holm & Westergård, 1930, *A. inexpectans* Kobayashi, 1938, *A. neglectus* Westergård, 1946, *A. exsulatus* Poulsen, 1960, *A. acutatus* (Ergaliev, 1980), and *A. lophotus* n. sp. (described below). *Acutatagnostus acutatus* Ergaliev (1980, pp. 91–92, pl. 11, figs 16, 17), the type species of *Acutatagnostus* Ergaliev, 1980, has the anterior part of the preglabellar median furrow effaced, but otherwise it conforms to the emended diagnosis of *Agnostus*. Because the preglabellar median furrow weakens forward in such species

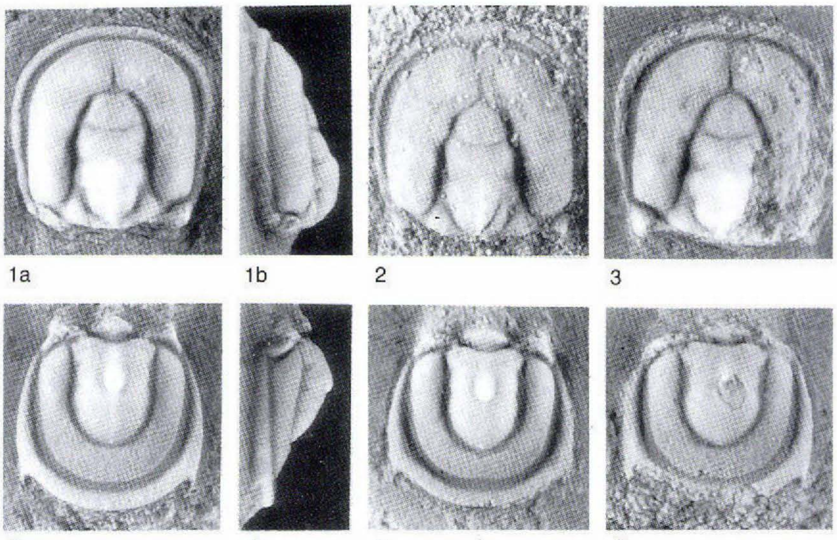


Fig. 5. *Agnostus lophotus* n. sp. All specimens from GGU 301313, unless otherwise stated, and all × 12. 1a, b, cephalon in dorsal and lateral views, MGUH 21.335. 2, latex cast of cephalon, MGUH 21.336 from GGU 313115. 3, cephalon, MGUH 21.337 from GGU 313115. 4a, b, holotype pygidium in dorsal and lateral views, MGUH 21.338. 5, 6, pygidia, MGUH 21.339 and 21.340.

as *A. lophotus* and *A. exsulatus,* anterior effacement of that furrow does not seem to warrant generic significance in *acutatus*. Therefore, I reassign the species to *Agnostus* and thereby suppress *Acutatagnostus* as a junior synonym. Other described species may warrant inclusion in *Agnostus*, but available morphological information, in my judgment, is equivocal.

Agnostus pisiformis is the only agnostoid for which appendages and soft anatomy are known (Müller & Walossek, 1987). The fidelity of preservation in the illustrated Swedish specimens is extraordinary, providing far greater detail than is known for any other trilobite species. In the absence of comparable information from other agnostoids, however, taxonomic evaluation of the many characters of the appendages and other soft parts of *Agnostus* remains moot.

The species here included in *Agnostus* have a composite observed stratigraphic range from the *Lejopyge laevigata* Zone (upper Middle Cambrian) to the *Pseudagnostus curtare* Zone (middle Upper Cambrian). Cephala assigned here as *Agnostus*? cf. *exsulatus* are from the upper *Ptychagnostus atavus* Zone, but their generic assignment is open to question.

Agnostus lophotus n. sp.

Fig. 5

Etymology. Greek *lophotos,* crested; referring to the carinate glabella.

Holotype. Pygidium (Fig. 5.4a, b), MGUH 21.338 from GGU 301313.

Material. More than 40 disarticulated cephala and pygidia are in GGU 301312, 301313, and 313115.

Diagnosis. Glabella laterally swollen behind F3 and having thread-like median carina behind median node. Axis of pygidium, relatively short, tumid; F1 and F2 nearly effaced.

Description. Agnostus with preglabellar median furrow weakening forward. Anteroglabella short, anteriorly rounded or ogival. Transglabellar furrow (F3) bowed posteriorly. Posteroglabella with thread-like median carina extending rearward from median node, near midlength, to occipital band; F1 and F2 weak abaxially; M3 laterally swollen, resulting in greatest glabellar width just behind F3. Genae smooth or having weak, irregular, scrobicular pits. Pygidium with deep, sagittally wide, posteriorly bowed, articulating furrow. Axis tumid and relatively short, with terminal secondary node; F1 and F2 nearly effaced; median tubercle prominent, slightly elongate; posterior margin broadly rounded. Pleural fields fairly uniform in width laterally and posteriorly. Border furrow moderately wide on glabella, moderate to wide on pygidium.

Remarks. A. lophotus closely resembles *A. neglectus* Westergård (1946, p. 85, pl. 13, figs 7–9), but differs from that species by having a preglabellar median furrow that weakens forward, a pygidial axis that is broader, shorter, and with more effaced ring furrows, and the pleural fields are more uniform in width.

Occurrence. All specimens are from basal beds of the Kap Stanton Formation in Peary Land, and are from the lower *Lejopyge laevigata* Zone.

Agnostus? cf. *exsulatus* Poulsen, 1960

Fig. 6

Remarks. Two small cephala, one each in GGU 319789 and 319790, resemble specimens of *A. exsulatus* Poulsen (1960, pl. 1, fig. 3; also Robison, 1988, fig. 7.5–8) by having a relatively short glabella and a preglabellar median furrow that weakens anteriorly. They differ, however, by having a narrower border furrow, straight rather than posteriorly bowed transglabellar furrow (F3), and more central placement of the median node on the posteroglabella. Whether these are ontogenetic or phylogenetic differences is difficult to judge from the small sample.

Occurrence. Both cephala are from the basal beds of the Kap Stanton Formation in Nyeboe Land, and from the upper *Ptychagnostus atavus* Zone. If further information, especially concerning the pygidium, supports assignment of this species to *Agnostus*, it will significantly extend downward the observed stratigraphic range of the genus.

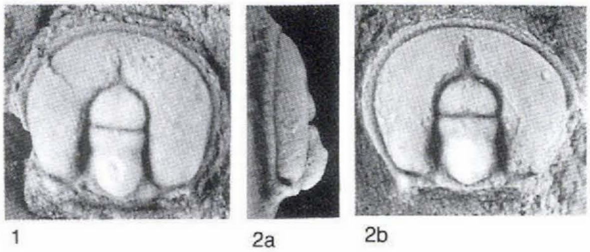


Fig. 6. *Agnostus*? cf. *exsulatus* Poulsen. 1, cephalon, MGUH 21.341 from GGU 319790, × 15. 2a, b, cephalon in lateral and dorsal views, MGUH 21.342 from GGU 319789, × 15.

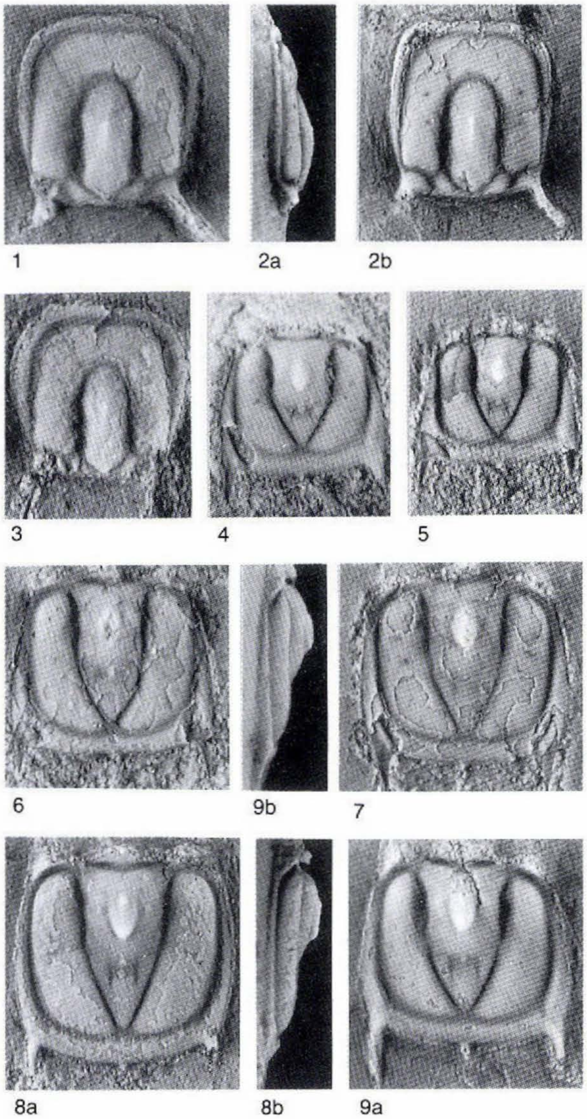


Fig. 7. *Clavagnostus* cf. *milli* Jago & Daily. All specimens from GGU 301313, unless otherwise stated, and all × 10. 1–3, cephala, MGUH 21.343–21.345. 4–7, 9, pygidia, MGUH 21.346–21.350. 8, pygidium, MGUH 21.351 from GGU 313115.

Family Clavagnostidae Howell, 1937
Genus *Clavagnostus* Howell, 1937

Type species. Agnostus repandus Westergård *in* Holm & Westergård 1930, pp. 13–15.

Remarks. Jago & Daily (1974) have reviewed the taxonomy of *Clavagnostus*. Their emended generic diagnosis is followed here, with the exception that not all specimens have smooth genae. Some previously illustrated specimens (e.g., Jago & Daily, 1974, pl. 11, figs 5–8, pl. 12, fig. 12) and some new specimens (Fig. 7) have weak scrobicular depressions or pits both on genae of the cephalon and pleural fields of the pygidium.

Clavagnostus cf. *milli* Jago & Daily, 1974
Fig. 7

Material. More than 40 specimens are in GGU 301312, 301313, and 313115.

Description of GGU specimens. Cephalon subquadrate with pair of long, divergent, border spines. Genae confluent (preglabellar median furrow absent). Glabella undivided, rounded anteriorly, angular posteriorly; median node anterior, weak, and carinate; width of glabella greatest at level of node. Pygidium subquadrate; border trispinose with pair of moderate-sized posterolateral spines and one tiny median spine. Axis lanceolate, unfurrowed, extending to posterior border furrow; median node large, may have superimposed smaller node on anterior surface; transverse sulcus of posteroaxis having pair of elongate pits and one or two secondary nodes. Surfaces of genae and pleural fields smooth or with weak scrobicular pits.

Remarks. Specimens from North Greenland closely resemble those from Tasmania that Jago & Daily (1974) assigned to *Clavagnostus milli*. They differ, however, in having a carinate node rather than a simple node on the glabella, and the tip of the pygidial axis is usually narrower. Jago & Daily did not mention a medial spine on the pygidial border, but at least one of their specimens (pl. 11, fig. 15) appears to have the broken stub of such a spine. All illustrated specimens of *C. milli* are rather poorly preserved and are taphonomically deformed, making it difficult to evaluate the taxonomic significance of these differences. The Tasmanian and Greenland specimens seem to be of approximately the same age. Whether or not their minor differences represent only geographic variation within a single species is unclear.

Clavagnostus trispinus Zhou & Yang (*in* Zhou *et al.*, 1977; see also Yang, 1978, pp. 17–18, pl. 1, fig. 2) from the lower *Lejopyge laevigata* Zone of China, which has a tiny median spine on the pygidial border, may be a junior synonym of *C. milli*. Poor preservation of all illustrated specimens of both taxa, however, hampers taxonomic evaluation. Moreover, a cephalon of *C. trispinus* has not been illustrated.

The Greenland specimens also closely resemble those of *C. repandus*, but differ by having a more quadrate pygidium, a more acuminate pygidial axis, and an additional spine on the pygidial border.

Occurrence. All of the Greenland specimens are from

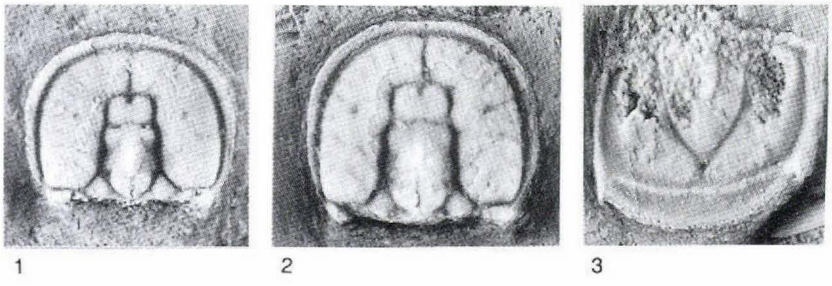


Fig. 8. *Diplagnostus planicauda* (Angelin). 1, 2, cephala, MGUH 21.352 and 21.353, from GGU 301313, × 12. 3, pygidium, MGUH 21.354 from GGU 298975, × 10.

basal beds of the Kap Stanton Formation in Peary Land, and are from the lower *Lejopyge laevigata* Zone.

Family Diplagnostidae Whitehouse, 1936
Genus *Diplagnostus* Jaekel, 1909

Type species. Agnostus planicauda Angelin, 1851, p. 7.

Diplagnostus planicauda (Angelin, 1851)
Fig. 8

New material. One pygidium is in GGU 298975, and 3 cephala and 1 pygidium are in GGU 301313.

Remarks. D. planicauda is a distinctive, geographically widespread, and stratigraphically long-ranging species. Its taxonomy was recently reviewed (Robison, 1988, pp. 33–35), and the new specimens add no new morphological information.

Lu & Lin (1989, pp. 76–77, pp. 202–203, pl. 2, fig. 15, pl. 3, figs 1–8) recently described and illustrated specimens from western Zhejiang, China, that were assigned to *Diplagnostus planicauda vestgothicus* (Wallerius), *D. zhexiensis* Lu & Lin, and *D. floralis* Öpik. Characters used to distinguish all these taxa fall within the range of variability observed within populations of *D. planicauda*, including ontogenetic series. Therefore, I consider the three taxa cited by Lu & Lin (1989) to be junior synonyms of *D. planicauda*.

Occurrence. D. planicauda was recently reported to range from near the base of the *Ptychagnostus punctuosus* Zone to near the top of the *Lejopyge laevigata* Zone (Robison, 1988, p. 35). Occurrences recorded by Egorova *et al.* (1982), Lu & Lin (1989), and Song (1989) indicate that the species actually ranges downward to at least the base of the *Ptychagnostus atavus* Zone. A representative pygidium of *D. planicauda* in GGU 298975 from Nyeboe Land (Fig. 8.3) is also from the *P. atavus* Zone. Other new specimens in GGU 301313 from Peary Land are from the *L. laevigata* Zone.

Genus *Iniospheniscus* Öpik, 1979

Type species. Iniospheniscus talis Öpik, 1979, pp. 50–51.

Remarks. Iniospheniscus is included in the Diplagnostidae with question because its pygidial border is not zonate, although medial expansion may indicate an incipient zonate condition. Also, compared with other genera in the family, the shape of its posteroaxis is unusual. The generic diagnosis of Shergold *et al.* (1990, p. 47) is followed here.

Iniospheniscus incanus? Öpik, 1979
Fig. 9.4

Remarks. A single, damaged pygidium in GGU 298969 from the upper Henson Gletscher Formation is assigned to *Iniospheniscus*. Its lateral margins converge slightly toward the posterior and it has a long, broad, pyriform axis that extends to the posterior border furrow. Its posterior border is medially widened. On the anteroaxis the F1 is weak, the F2 is effaced, and the median tubercle is large and elongate. The posteroaxis is laterally expanded and subpentagonal in outline. The acrolobe is slightly constricted, the border furrow is wider laterally than it is posteriorly, and the border has a pair of small posterolateral spines. These characters are similar to those of *I. incanus* Öpik (1979, p. 51, pl. 9, figs 8, 9) from Australia, but the pygidial axis is slightly broader and the lateral borders are narrower. Assignment of the new pygidium to *I. incanus* is questioned, primarily because information about the entire exoskeleton is limited. The new pygidium is from the *Ptychagnostus atavus* Zone, as are all described specimens of *I. incanus*.

Genus *Linguagnostus* Kobayashi, 1939

Type species. Agnostus kjerulfi Brøgger, 1878, pp. 49–50.

Remarks. The generic diagnosis of Shergold *et al.* (1990, pp. 47–48) is followed here.

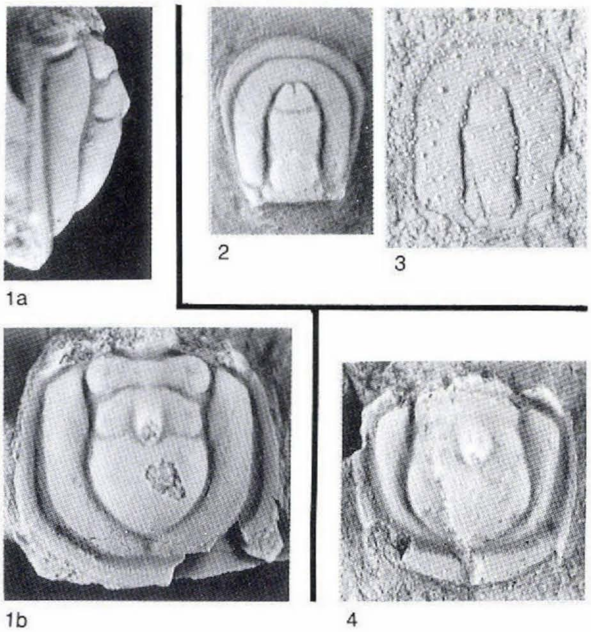


Fig. 9. Undetermined agnostoids and *Iniospheniscus*.

1a, b, Genus and species undetermined 1. Lateral and dorsal views of pygidium, MGUH 21.355 from GGU 298970, × 8.

2, 3, Genus and species undetermined 2. 2, cephalon, MGUH 21.356 from GGU 298970, × 10. 3, cephalon, MGUH 21.357 from GGU 298969, × 10.

4, *Iniospheniscus incanus*? Öpik, pygidium, MGUH 21.358 from GGU 298969, × 10.

Linguagnostus groenwalli Kobayashi, 1939

Fig. 10

Agnostus kjerulfi Brøgger, Grönwall, 1902, pp. 69–70, pl. 1, fig. 11

Linguagnostus kjerulfi forma *grönwalli*, Kobayashi, 1939, pp. 142–143

Linguagnostus grönwalli Kobayashi, Westergård, 1946, pp. 63–64, pl. 8, figs 30a, b; Pokrovskaya *in* Chernysheva, 1960, pl. 1, fig. 5; Egorova, Pegel & Chernysheva *in* Egorova *et al.*, 1982, p. 62, pl. 12, fig. 3, pl. 14, fig. 6, pl. 16, figs 11, 12

New material. Four cephala and 6 pygidia are in GGU 319789 and 319790.

Emended diagnosis. Cephalon having narrow border and very wide, shallow border furrow; acrolobe unconstricted. Glabella broad, subcylindrical; width of anteroglabella about twice its length; F3 shallow, narrow, straight or slightly bowed rearward; posteroglabella with carinate median node anterior from midpoint. Thorax having wide axis. Pygidium zonate in late holaspid period; collar thread-like, bowing forward onto posterior border furrow. Acrolobe constricted and bordered posteriorly by narrow sinuous ridge that fades posterolaterally into prong-like projections extending toward border spines. Axis broad; F1 and F2 mostly effaced; anteroaxis subquadrate with carinate tubercle mostly confined to M2; posteroaxis having well-developed transverse sulcus and associated secondary median node near anterior margin, part behind sulcus reduced to small triangular vestige. Pleural fields narrow between axis and posterior border furrow, having pair of low, transversely elongate swellings that may be separated by postaxial depression

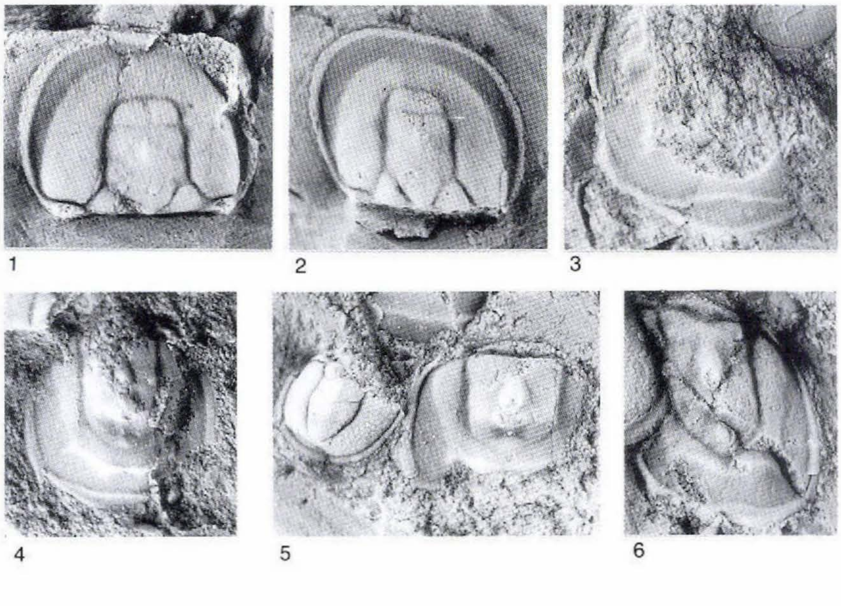


Fig. 10. *Linguagnostus groenwalli* Kobayashi. 1, cephalon, MGUH 21.359 from GGU 319790, × 5.5. 2, cephalon from MGUH 21.360 from GGU 319789, × 6. 3, incomplete pygidium, MGUH 21.361 from GGU 319790, × 6. 4, latex cast of pygidium, MGUH 21.362 from GGU 319789, × 6. 5, incomplete pygidium associated with smaller pygidium of *Ptychagnostus affinis* (left), MGUH 21.363 from GGU 319790, × 6. 6, deformed pygidium, MGUH 21.364 from GGU 319790, × 6.

or furrow. Pygidial border furrow very wide, shallow, and irregular in width; border narrow, bispinose.

Remarks. The few new specimens of this species are fragmentary or deformed, or both. Nevertheless, their number and condition is sufficient to demonstrate most characters of the cephalon and pygidium. Such diagnostic characters of the pygidium as advanced effacement of ring furrows, a carinate tubercle mostly confined to the second ring, shape of the acrolobe, and a pair of low swellings between the axis and posterior border furrow, closely match those of rare and small specimens of *Linguagnostus groenwalli* from Scandinavia (Westergård, 1946, pp. 63–64). Most of the pygidia from Greenland are larger than those previously described from Scandinavia, however, and have a shallow postaxial depression rather than a median furrow, a wider border furrow, and a pygidial collar (*sensu* Öpik, 1967, p. 62). All of these differences are likely to be of ontogenetic origin, and the new specimens are therefore assigned to *L. groenwalli.*

In discussing *Linguagnostus,* Öpik (1979, p. 52) concluded that *L. groenwalli* "is an aberrant form with a nonzonate pygidium" that "cannot be convincingly accommodated in this [*Linguagnostus*] or any other genus of Diplagnostidae." With the discovery in Siberia (Egorova *et al.*, 1982, pl. 14, fig. 6) and Greenland of larger specimens having a zonate pygidial border, *L. groenwalli* now accords well with a recent diagnosis of *Linguagnostus* (Shergold *et al.*, 1990, pp. 47–48). As size increases, the larger holaspid pygidia show progressively greater separation of the posterior border and the narrow but distinct collar (Fig. 10.3, 4, 6). Comparison of new specimens indicates that the ontogenetic appearance of a collar in *L. groenwalli* was delayed until the middle of the holaspid period.

The transverse ridge on the posterior border furrow of *L. groenwalli* (Fig. 10.3, 4, 6) and the ridge separating the posterior acrolobe and border furrow of *L. kjerulfi* (e.g., Westergård, 1946, pl. 8, fig. 32) both fall within the definition of a pygidial collar (*sensu* Öpik, 1967, p. 62; Shergold *et al.*, 1990, p. 16). Two separate ridges on pygidia in Fig. 10.4 and 10.6 demonstrate that some ridges previously identified as pygidial collars are not homologous. Better preserved specimens should help to evaluate the relationship and significance of these ridges.

Occurrence. L. groenwalli has been reported from the *Ptychagnostus punctuosus* Zone of Denmark and Sweden, as well as approximately correlative levels in the *Anapolenus* Zone of Russia (Siberia). New specimens from Greenland are all from the basal beds of the Kap Stanton Formation in Nyeboe Land, and are from the upper *Ptychagnostus atavus* Zone.

Family Doryagnostidae Shergold *et al.*, 1990

Emended diagnosis. Agnostoids with preglabellar median furrow variably developed. Border furrow may expand as small triangular depression (deltoid area) at junction with preglabellar median furrow. Axial furrow well developed. Glabella cylindrical to slightly tapered, unequally divided by transglabellar furrow (F3), rounded posteriorly. Basal lobes simple. Genae smooth. Pygidium axiolobate and simplimarginate. Axis terminating short of posterior border furrow; F1 and F2 undeveloped or weakly developed only near axial furrow. Anteroaxis with node on M2. Posteroaxis lanceolate to weakly ogival, commonly with acuminate tip; transverse sulcus and secondary node appearing during phylogeny. Postaxial median furrow present. Margin of pygidium rounded posteriorly, bispinose. Cephalic and pygidial border furrows of moderate width.

Remarks. The subfamily Doryagnostinae was erected by Shergold et al. (1990, p. 44), who assigned it to the family Spinagnostidae Howell, 1935a. From review of the type collection of *Spinagnostus franklinensis* Howell, 1935a, the type species of *Spinagnostus,* it is noted that the specimens are from multiple localities, all are disarticulated, and all are poorly preserved. In my opinion, the specimens lack diagnostic characters for differentiation at the generic and family level, and a question about the correct association of disarticulated parts is open. Therefore, I consider both *Spinagnostus* and Spinagnostidae to be unrecognisable taxa.

As emended below, the inferred ancestral species of *Doryagnostus*, *D. vinicensis* (Šnajdr, 1957), seemingly evolved from *Peronopsis gaspensis* Rasetti, 1948 by development of a preglabellar median furrow (Robison, 1978). A similar furrow, apparently from iterative evolution, is also present in such genera as *Agnostus* and *Ptychagnostus*. Based on the inferred phylogeny of *Doryagnostus,* I concur with Shergold *et al.* (1990) in assigning it to a separate family-group taxon, but I here elevate it from subfamily to family rank. Such rank corresponds to that of the Ptychagnostidae, which is inferred to have arisen from *Peronopsis brighamensis* Resser, 1939 by independent evolution of a preglabellar median furrow (Robison, 1978).

Without discussion, Shergold *et al.* (1990, pp. 44–45) assigned *Doryagnostus* Kobayashi, 1939, *Itagnostus* Öpik, 1979, and *Rhodotypiscus* Öpik, 1979 to their Doryagnostinae. Of these genera, I consider *Itagnostus* to be a junior synonym of *Peronopsis.* The type species of *Itagnostus, Agnostus elkedraensis* Etheridge, 1902, lacks any reported evidence of a preglabellar median furrow.

Moreover, it differs from *Peronopsis montis* (Matthew, 1899) by only its slightly more posterior median node on the glabella and slightly more quadrate cephalon and pygidium. Whether these differences are genotypic or phenotypic is problematic, but in my opinion they lack generic significance. An emended diagnosis of *Peronopsis* is given below, which is broader in concept than that of Shergold *et al.* (1990). The type species of *Rhodotypiscus, R. nasonis* Öpik, 1979 has an incomplete preglabellar median furrow. A preglabellar median furrow is variably developed in *Doryagnostus vinicensis* (Šnajdr, 1957, emended below), and commonly it is incomplete in some populations (e.g., Robison, 1978, pp. 8–9). All other characters of *R. nasonis* are shared with representative species of *Doryagnostus*, and *Rhodotypiscus* is therefore suppressed as a subjective junior synonym. With these taxonomic emendations, *Doryagnostus* is the only genus presently assigned to the Doryagnostidae.

Doryagnostids can usually be distinguished from furrowed ptychagnostids by lesser development of pygidial ring furrows. Also, some doryagnostids have a deltoid area on the cephalon, which is absent on ptychagnostids. Effacement of furrows on the acrolobes is a common evolutionary trend in ptychagnostids, but has not been reported in doryagnostids.

Genus *Doryagnostus* Kobayashi, 1939

Doryagnostus Kobayashi, 1939, p. 148; Robison, 1978, p. 5 (synonymy to date); Öpik, 1979, pp. 81–82; Shergold *et al.*, 1990, pp. 44–45

Ceratagnostus Whitehouse, 1939, pp. 255–256

Rhodotypiscus Öpik, 1979, p. 79; Shergold *et al.*, 1990, p. 45

Type species. Agnostus incertus Brøgger, 1878, pp. 70–71.

Emended diagnosis. As for family.

Remarks. Species here included in *Doryagnostus* are *D. incertus* (Brøgger, 1878) (= *Ceratagnostus magister* Whitehouse, 1939), *D. vinicensis* (Šnajdr, 1957; see synonymy below), *D. deltoides* Robison *in* Jell & Robison, 1978 (= *D. notalibrae* Öpik, 1979), *D. nasonensis* (Öpik, 1979), *D. solidus* Öpik, 1979, *D. sayramhuensis* (Zhang, 1981), and *D. sectilis* Xiang & Zhang, 1985. Reasons for and against the synonymy of *D. incertus* and *D. magister* have been discussed by Robison (1978, p. 7) and Nikolaisen & Henningsmoen (1990, p. 61).

Öpik (1979, p. 82) observed that a species of *Doryagnostus*, possibly new, is present in Utah, and is represented by some specimens that I previously illustrated (Robison, 1964, pl. 79, figs 8, 11) as ?*Ptychagnostus* sp. and *Ptychagnostus hybridus*. I concur, but a search for additional specimens has not been successful.

Doryagnostus vinicensis (Šnajdr, 1957)

Fig. 11

Ptychagnostus (*Triplagnostus*) *vinicensis* Šnajdr, 1957, p. 235, pl. 1, fig. 1; Šnajdr, 1958 (in part), pp. 71–72, pp. 243–244, pl. 4, figs 21, ?22 (not pl. 4, figs 19, 20, 23, 24)

Doryagnostus wasatchensis Robison, 1978, pp. 8–9, pl. 1, figs 1–4, 6; pl. 2, figs 6, 9–13

Triplagnostus vinicensis (Šnajdr), Fatka *et al.*, 1981, pp. 367–368, pl. 1, fig. 1, pl. 2, figs 6, 7

Doryagnostus vinicensis (Šnajdr), Fatka & Kordule, 1992, pl. 2, fig. 4

New material. More than 20 disarticulated cephala and pygidia are in GGU 298970.

Emended diagnosis. Doryagnostus having relatively broad glabella, its width being about equal to or slightly greater than that of adjacent genae at level of F3. Anteroglabella large and broadly rounded to obtusely pointed at front. Posteroglabella tumid at rear, with median node behind midpoint. Pygidium characterised by small border spines. Posteroaxis lanceolate to slightly ogival, and usually without transverse sulcus.

Remarks. Several new specimens from North Greenland

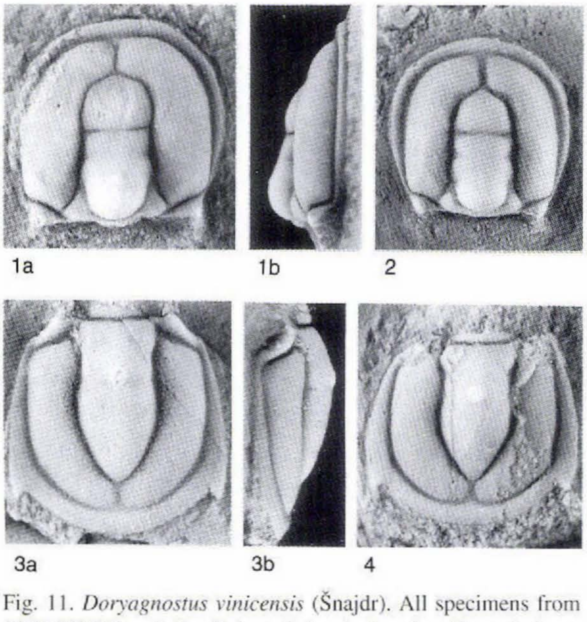


Fig. 11. *Doryagnostus vinicensis* (Šnajdr). All specimens from GGU 298970 and all × 8. 1, cephalon in dorsal and lateral views, MGUH 21.365. 2, cephalon, MGUH 21.366. 3, pygidium in dorsal and lateral views, MGUH 21.367. 4, pygidium, MGUH 21.368.

have characters that accord closely with the emended diagnosis of *D. vinicensis.*

The original description of *Ptychagnostus* (*Triplagnostus*) *vinicensis* was confused because it was based in part on a holotype cephalon of *Doryagnostus* and in part on pygidia of *Lejopyge hybridus,* as here reassigned. With the aid of additional specimens, some complete, that erroneous association of sclerites was recognised by Fatka *et al.* (1981), but the species was assigned to *Triplagnostus.* In subsequent discussion of new localities by Fatka & Kordule (1992), however, the species was reassigned without taxonomic comment to *Doryagnostus.*

Doryagnostus wasatchensis Robison, 1978, which was described from Utah, is now considered to be a subjective junior synonym of *D. vinicensis.* Minor differences between the type specimens of these taxa seem to have been accentuated by taphonomic processes. On one hand, the illustrated specimens from Czechoslovakia are preserved as moulds in shale and show internal features of the exoskeleton. On the other hand, the illustrated specimens from Utah are preserved in limestone and show external features of the exoskeleton.

The preglabellar median furrow is variably developed in observed populations from Utah, but is uniformly present in known specimens from Czechoslovakia and Greenland. The more variable specimens from Utah are inferred to represent an earlier stage of phylogeny.

Occurrence. The new specimens are from the middle Henson Gletscher Formation, and are from the *Ptychagnostus gibbus* Zone. The species has been reported elsewhere from the *Eccaparadoxides pusillus* Zone of Czechoslovakia and the upper *P. gibbus* Zone of the United States (Utah).

Family Metagnostidae Jaekel, 1909

Genus *Diplorrhina* Hawle & Corda, 1847

Diplorrhina Hawle & Corda, 1847, pp. 46–47; Lermontova, 1940, p. 123; Öpik, 1967, pp. 75–76; Pek & Vaněk, 1971, pp. 271–272; Shergold *et al.*, 1990, p. 46
Mesospheniscus Hawle & Corda, 1847, p. 46
Quadragnostus Howell, 1935a, p. 219; Howell *in* Harrington *et al.*, 1959, p. O186; Shaw, 1966, p. 849; Shergold *et al.*, 1990, p. 56
?*Pseudoperonopsis* Harrington, 1938, p. 151; Shergold *et al.*, 1990, p. 45

Type species. Diplorrhina triplicata Hawle & Corda, 1847, p. 47; subsequent designation by Pek & Vaněk, 1971, p. 271 [= *Battus cuneifer* Barrande, 1846, p. 18].

Emended diagnosis. Cephalon commonly subquadrate. Glabella subcylindrical, length about two-thirds that of cephalon, broadly angular at posterior; F3 well developed to effaced, bowed rearward if developed, commonly weakening abaxially. Anteroglabella short, subcircular to elliptical. Posteroglabella laterally swollen at anterior M3, slightly constricted at F2; median node near anterior edge of M2. Basal lobes simple, anteriorly indenting glabella. Genae confluent, smooth to scrobiculate. Thorax unmodified. Pygidium axiolobate and simplimarginate; width greater than length. Axis moderately long to long; F1 and F2 weak or effaced; median tubercle moderate in size, commonly elongate. Posteroaxis, if elongate, having weak transverse sulcus and secondary median node. Pleural fields smooth. Border flat, widening posterolaterally into pair of marginal spines.

Remarks. The generic names *Diplorrhina* and *Mesospheniscus,* here considered to be synonyms, were first published on the same page by Hawle & Corda (1847, p. 46). Eleven species were assigned to *Diplorrhina* by Hawle & Corda (1847, pp. 47–50), and from these Pek & Vaněk (1971, p. 271) subsequently designated *D. triplicata* as the type species. The type species of *Mesospheniscus* by monotypy is *Battus cuneifer* Barrande, 1846. Lectotypes for both *D. triplicata* and *B. cuneifer* were selected by Šnajdr (1958, pl. 3, fig. 9 and pl. 2, fig. 30, respectively), but he reassigned *cuneifer* to *Peronopsis,* and he listed *triplicata* as a junior synonym of *P. cuneifer.* Genal surfaces of specimens illustrated by Šnajdr as *P. cuneifer* vary from smooth to moderately scrobiculate, which he attributed to 'pelomorphic' deformation (compare Pek & Vaněk, 1971, p. 271). After further study of the same specimens, Pek & Vaněk (1971) reassigned those with smooth genae to *Peronopsis cuneifer* and those with scrobiculate genae to *Diplorrhina triplicata.*

New specimens from North Greenland have characters similar to those of specimens illustrated by Šnajdr (1958) as *Peronopsis cuneifera,* including genae that grade from smooth to moderately scrobiculate (see Fig. 12.1–5). Such scrobiculation is here judged to be a primary character rather than a secondary condition resulting from taphonomic processes. Therefore, based on the apparent variability in scrobiculation, in combination with shared characters of the axial lobe and borders, I agree with Šnajdr (1958) that *D. triplicata* Hawle & Corda, 1847 is a junior synonym of *Battus cuneifer* Barrande, 1846.

Some authors, including myself (Robison, 1964, p. 529), have previously considered *Diplorrhina* and *Mesospheniscus* to be synonyms of *Peronopsis.* Based on new material and further analysis, I now consider *Diplorrhina* and *Mesospheniscus* to be synonyms because of the synonymy of their type species, but not synonyms of *Peronopsis.* Because such taxonomy has not been previously suggested, I follow the Principle of the First Reviser (International Code of Zoological Nomenclature, 1985, Article 24) and here select *Diplorrhina* to have precedence as the senior synonym. This choice is influenced by the fact that the lectotype of *D. triplicata,* the type species of *Diplorrhina*, is a complete holaspid (Šnajdr, 1958, pl. 4, fig. 9) with a full complement of differential characters. In comparison, the lectotype of *Battus cuneifer* Barrande, the type species of *Mesospheniscus,* is a meraspid stage 0 instar (Šnajdr, 1958, pl. 3, fig. 30) with few differential characters.

Diplorrhina, as emended, is characterised by a posteriorly bowed glabellar F3, anterolateral swelling of the glabellar M3, and a flattened, posterolaterally expanded, spinose pygidial border. All of these characters may be weakly developed or absent in early instars, and were generally accentuated during ontogeny. Length of the pygidial axis seems to have increased during phylogeny, commonly reaching almost to the posterior border furrow. With elongation, the posteroaxis developed a weak transverse sulcus with a secondary median node. Size of the pygidial spines also increased during phylogeny, primarily by increase in basal width. Expression of segmental furrows on the axial lobe and development of genal scrobiculation are both variable.

Among species here assigned or reassigned to *Diplorrhina* are *Battus cuneifer* Barrande, 1846, *Agnostus quadratus* Tullberg, 1880, *Quadragnostus solus* Howell, 1935a, *Peronopsis cylindrica* Westergård, 1946, *Peronopsis scaphoa* Öpik, 1961, and *Diplorrhina oncota* n. sp. Other representatives of *Diplorrhina* are *D. redita* Pek & Vaněk, 1971 (pp. 274–275, pl. 1, figs 4, 5), which may be a junior synonym of *D. cuneifer,* and *Peronopsis fallax depressa* Westergård, 1946 (pp. 27–38, pl. 2, figs 25, 26), which may be a junior synonym of *D. cylindrica.* The origin of *Diplorrhina* is unclear, but comparative morphology and stratigraphic ranges suggest that it arose by cladogenesis from either *Peronopsis fallax* or *Peronopsis ferox.*

Specimens of *Q. solus* Howell, the type species of *Quadragnostus* Howell, 1935a, have been previously illustrated with only retouched photographs (Howell, 1935a, pl. 22, figs 6, 7; Howell *in* Harrington *et al.*, 1959, fig. 126.6a, b) that convey false information about characters. The same specimens, which include the holotype pygidium and a paratype cephalon, are illustrated here with unaltered photographs (see Fig. 13). Although poorly preserved, these specimens appear to possess the differential characters of *Diplorrhina*, and therefore *Quadragnostus* is considered to be a junior synonym.

Another species of *Diplorrhina* seems to be represented by poorly preserved specimens having a slightly shorter pygidial axis than do the species mentioned above. Some such specimens from France have been assigned to *Peronopsis sallesi* (Munier-Chalmas & Bergeron) by Howell (1935b, pp. 226–227, pl. 22, figs 17, 18?). Other specimens from Spain and France have been assigned to *Peronopsis fallax sallesi* by Sdzuy (1961, pp. 523–524, pl. 2, figs 1–8), Courtessole (1973, pp. 116–117, pl. 2, figs 4–14), and Gil Cid (1981, pp. 118–119). Similar specimens from northern Norway have been assigned to *Peronopsis ferox sallesi* by Nikolaisen & Henningsmoen (1990, pp. 57–59, fig. 6.A-G). Although most of these specimens appear to represent *Diplorrhina*, the species name is in question because the type specimen of *Agnostus sallesi* Munier-Chalmas & Bergeron *in* Bergeron, 1889 is assumed to be lost (Laurie, 1990, p. 319). This has further taxonomic implications because *A. sallesi* is the type species of *Pseudoperonopsis* Harrington, 1938. The taxonomic affinity of *Pseudoperonopsis* is therefore difficult to evaluate without more knowledge about characters of the type specimen of *A. sallesi,* and the genus is listed here as a questionable synonym of *Diplorrhina.*

Most characters of *Diplorrhina* are closely similar to those of the Metagnostidae (*sensu* Fortey, 1980, pp. 24–29) of Ordovician age. A notable exception is the longer axis on the pygidium of *Diplorrhina.* Based on these similarities, I suggest that the metagnostids may have originated from *Diplorrhina*, and that one change in the transitional lineage was reduction of the posteroaxis behind the transverse sulcus. More information from Late Cambrian agnostoids is needed to test this hypothesis. In the meantime, *Diplorrhina* is questionably assigned to the Metagnostidae as its ancestral genus. Variable development of genal scrobiculation in *Diplorrhina* may be significant because metagnostids are the only Ordovician agnostoids having that character.

Diplorrhina, as emended, is known from Czechoslovakia, Sweden, Norway, Denmark, England, France, Spain, Russia (Siberia), Australia (Queensland), the United States (Vermont), Canada (eastern Newfoundland), and Greenland. It has an observed stratigraphic range from the *Ptychagnostus atavus* Zone to the lower *Lejopyge laevigata* Zone, and questionably from the upper *Ptychagnostus gibbus* Zone.

Diplorrhina oncota n. sp.

Fig. 12

Etymology. Greek *onkotos,* swollen; referring to the anterolateral swelling of the glabellar M3.

Holotype. Cephalon (Fig. 12.1a-c), MGUH 21.369 from GGU 301313.

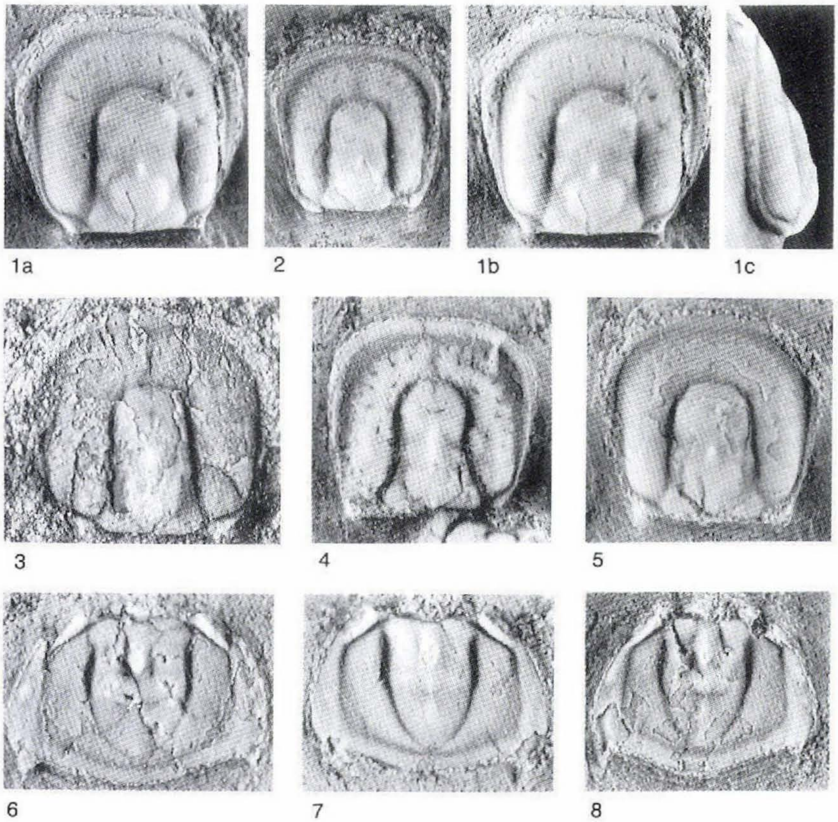


Fig. 12. *Diplorrhina oncota* n. sp. All specimens from GGU 301313 and all × 10, unless otherwise stated; relative width of the pygidia has probably been accentuated by taphonomic compression. 1, holotype cephalon in dorsal (a, b, stereogram) and lateral (c) views, MGUH 21.369. 2, 4, 5 cephala, MGUH 21.370–21.372. 3, cephalon, MGUH 21.373 from GGU 313115, × 8. 6, 8, pygidia, MGUH 21.374 and 21.375 from GGU 313115. 7, pygidium, MGUH 21.376.

Material. More than 20 specimens are in GGU 301313 and 313115.

Diagnosis. Diplorrhina with glabellar F3 effaced or with only medial development, and M3 prominently swollen at anterolateral corners. Genae smooth to moderately scrobiculate. Pygidium wider than long; axis subcylindrical forward of transverse sulcus, but weakly constricted at M2; F1 and F2 mostly effaced; posteroaxis tapers to broadly rounded point behind transverse sulcus. Lateral pygidial borders unusually wide and flat.

Remarks. D. oncota most closely resembles *D. cuneifer* (Šnajdr, 1958, pl. 3, figs 13–37, pl. 4, figs 1–11) and *D. cylindrica* (Westergård, 1946, pl. 3, figs 17–21) but differs from both by having a smaller anteroglabella, common effacement of the glabellar F3, and greater effacement of ring furrows on the pygidium. *D. cuneifer* mainly differs from *D. cylindrica* by having more scrobiculae and a larger median tubercle on the pygidium.

D. solus (Howell, 1935a) is based on poorly preserved specimens (Fig. 13) that differ little from those of *D. quadrata* (Tullberg, 1880), and *D. solus* may be a junior synonym. Those two taxa are easily differentiated from *D. oncota* by their more evenly tapered pygidial axis and better developed glabellar F3.

Occurrence. All specimens of *D. oncota* are from basal beds of the Kap Stanton Formation in Peary Land, and are from the lower *Lejopyge laevigata* Zone.

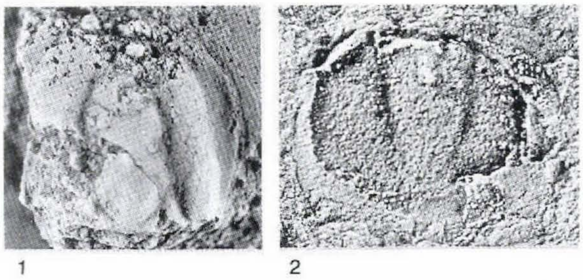


Fig. 13. *Diplorrhina solus* (Howell) from the St. Albans Shale of Vermont. 1, paratype cephalon, Princeton University no. 40126, × 5. 2, holotype pygidium, Princeton University no. 9793, × 5.

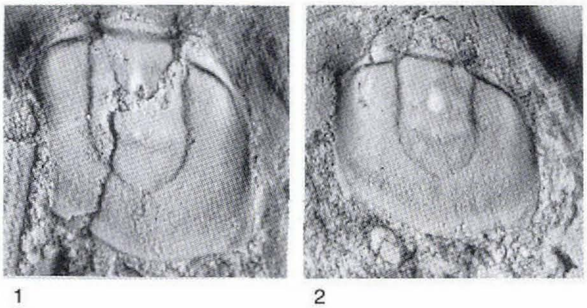


Fig. 14. *Diplorrhina* cf. *sallesi* (Munier-Chalmas & Bergeron) from GGU 319789. 1, 2, pygidia, MGUH 21.377 and 21.378, both × 8.

Diplorrhina cf. *sallesi* (Munier-Chalmas & Bergeron *in* Bergeron (1889)

Fig. 14

Remarks. The taxonomy of *D. sallesi,* as reassigned here, has been recently reviewed by Nikolaisen & Henningsmoen (1990, pp. 57–59), who referred the taxon to *Peronopsis ferox sallesi.* Two pygidia in GGU 319789 closely resemble those previously assigned to the taxon (for synonymy, see Nikolaisen & Henningsmoen, 1990, pp. 57–58), but their assignment to genus and species is open to question in the absence of associated cephala. Although seemingly affected by taphonomic compression, the two pygidia show the characteristic axial form of *D. sallesi* and such other features as effaced ring furrows, moderate-sized median tubercle, sulcate posteroaxis, and robust border spines (indicated by broken stubs). The specimens are from basal beds of the Kap Stanton Formation in Nyeboe Land, and are from the upper *Ptychagnostus atavus* Zone.

Family Peronopsidae Westergård, 1936

Genus *Hypagnostus* Jaekel, 1909

Type species. Agnostus parvifrons Linnarsson, 1869, p. 82.

Hypagnostus brevifrons (Angelin, 1851)

Fig. 15

Agnostus brevifrons Angelin, 1851, p. 6, pl. 6, fig. 4; Brøgger, 1878, pp. 57–58, pl. 6, fig. 10; Tullberg, 1880, pp. 35–36, pl. 2, fig. 29a, b; Grönwall, 1902, p. 76

Metagnostus brevifrons (Angelin), Jaekel, 1909, p. 399

Hypagnostus brevifrons (Angelin), Whitehouse, 1936, p. 104; Kobayashi, 1939, p. 123, 125; Whitehouse, 1939, pp. 263–264; Westergård, 1946, pp. 48–49, pl. 5, figs 24–29; Öpik, 1961, pp. 58–59, pl. 18, figs 6–10; Wang et al., 1963, p. 27, pl. 2, figs 12–15; Lu *et al.*, 1965, pp. 44–45, pl. 4, figs 21–24; Khajrullina, 1970, p. 13, pl. 1, fig. 2; Khajrullina, 1973, pp. 42–44, pl. 2, figs 6, 9, ll, 12; Repina *et al.*, 1975, p. 116, pl. 10, figs 7–10, pl. 11, figs 1–3; Rosova, 1977, p. 166, pl. 23, figs 9–12; Ergaliev, 1980, pl. 4, figs 9–11; Yang, 1982, pl. 2, figs 6, 7; Egorova, Pegel & Chernysheva *in* Egorova *et al.*, 1982, p. 70, pl. 18, fig. 5, pl. 21, figs 3, 5, pl. 34, fig. 17, pl. 46, fig. 2a; Xiang & Zhang, 1985, p. 67, pl. 17, figs 11, 12; Lu & Lin, 1989, pp. 106–107, 223, pl. 11, figs 1, 2

Cyclopagnostus brevifrons (Angelin), Howell, 1937, p. 1166; Öpik, 1979, p. 66

Hypagnostus brevifrons vulgarus Qian & Qiu *in* Qiu *et al.*, 1983, p. 41, pl. 14, figs 5, 6

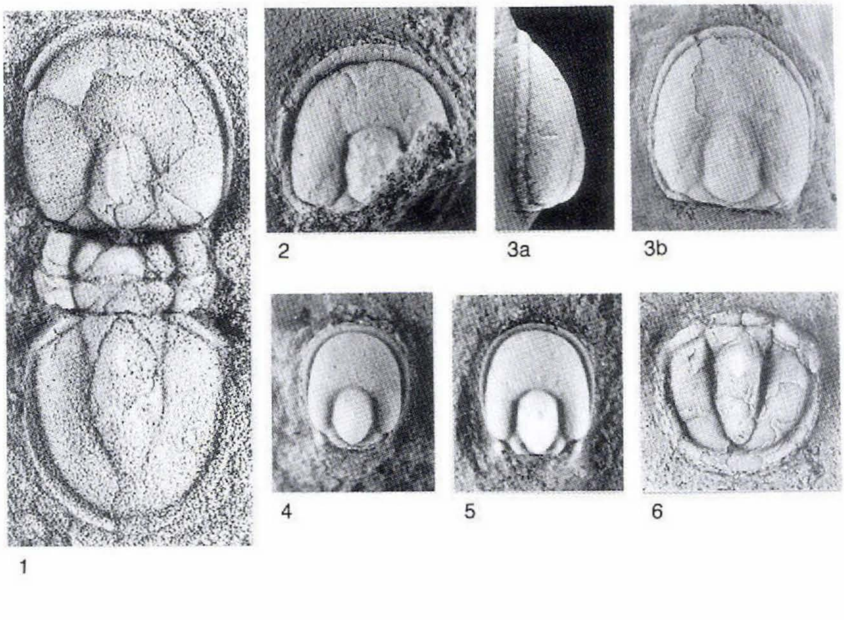


Fig. 15. *Hypagnostus brevifrons* (Angelin). All specimens from GGU 313115, unless stated otherwise. 1, dorsal exoskeleton, MGUH 21.379, × 5. 2, incomplete cephalon, MGUH 21.380, × 10. 3a, b, cephalon in lateral and dorsal views, MGUH 21.381, × 8. 4, cephalon, MGUH 21.382, × 15. 5, cephalon, MGUH 21.383 from GGU 301313, × 15. 6, pygidium, MGUH 21.384, × 10.

New material. Thirteen specimens are in GGU 301312, 301313, and 313115.

Emended diagnosis. Hypagnostus with short, anteriorly tapering remnant glabella; length less than half that of cephalon. Pygidial axis unfurrowed, well separated from posterior border furrow in late holaspid period; posteroaxis varies from subcylindrical with broadly rounded rear to moderately tapered. Pleural fields confluent in larger holaspides. Posterior border uniform in width.

Remarks. H. brevifrons differs from *H. parvifrons*, the type species of *Hypagnostus*, by its shorter pygidial axis in the late holaspid period and by lacking a medial expansion of the posterior border. Also, its glabella is usually more tapered.

The new specimens from Greenland have a considerable range in holaspid size and show some related changes in morphology. For example, the anterior glabella usually is more tapered on larger holaspid cephala (compare Fig. 15.1–5). On the pygidium, the axis extends almost to the posterior border furrow on smaller holaspides (Fig. 15.6), but is well separated on large holaspides (Fig. 15.1).

Howell (1937) described *Cyclopagnostus hesperius* as a new genus and new species. At the same time, he reassigned *Agnostus brevifrons* Angelin to *Cyclopagnostus*, and both taxa were assigned to the new subfamily Cyclopagnostinae and new family Cyclopagnostidae. Soon after, Kobayashi (1939, pp. 123, 127–128) suppressed *Cyclopagnostus* as a junior synonym of *Hypagnostus*. That synonymy has been generally accepted, although Howell *in* Harrington *et al.* (1959, p. O175) and Öpik (1979, p. 66), both without explanation, continued to recognise *Cyclopagnostus* as a valid genus. For comparison with *H. brevifrons*, the type specimens of *C. hesperius* are here reillustrated with photographs that are not retouched (Fig. 16). From review of these types, I conclude that the holotype of *C. hesperius* (Fig. 16.2) is an agnostoid, but its characters are inadequate for identification at lower taxonomic levels. The holotype was identified by Howell as a pygidium, but even that determination, in my opinion, is not entirely certain. The only previously illustrated paratype (Fig. 16.1) is a cephalon with characters similar to specimens of *Hypagnostus*, but Howell's handwritten label indicates that it is from a different locality than the holotype. Assignment of these two types to the same species cannot be verified, and the holotype lacks definitive characters. Therefore, I suggest that the name *Cyclopagnostus hesperius* be restricted to the holotype, and that *Cyclopagnostus* be regarded as an unrecognisable agnostoid genus.

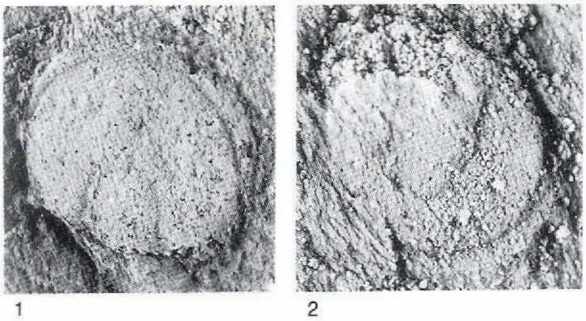


Fig. 16. *Cyclopagnostus hesperius* Howell from the St. Albans Shale of Vermont. 1, paratype cephalon, Princeton University no. 9797, × 8. 2, latex cast of holotype, probably a pygidium, Princeton University no. 9796, × 8.

Occurrence. H. brevifrons is cosmopolitan in open-marine lithofacies. Its observed stratigraphic range is from at least the middle *Ptychagnostus punctuosus* Zone to the middle *Lejopyge laevigata* Zone. All new specimens are from basal beds of the Kap Stanton Formation in Peary Land, and are from the lower *L. laevigata* Zone.

Hypagnostus parvifrons (Linnarsson, 1869)

Fig. 17

New material. Three cephala and 4 pygidia are in GGU 298969, 319789, and 319790.

Remarks. H. parvifrons is a common agnostoid species (e.g., Westergård, 1946, p. 45; Robison, 1964, p. 529; Öpik, 1979, pp. 66–67; Egorova *et al.*, 1982, p. 69; Zhang & Jell, 1987, p. 43–44; Sun, 1989, pp. 89–90; Samson *et al.*, 1990, p. 1466) with cosmopolitan distribution in open-marine lithofacies. It is characterised by a glabellar length less than half that of the cephalon, an unfurrowed and moderately tumid pygidial axis, and a posteriorly widened pygidial border with a medial forward projection. The axis commonly extends to meet the medial projection of the border, but the two may connect by a short postaxial furrow. The new specimens from Greenland, like many from North America, have a shorter axis and a short postaxial median furrow.

Occurrence. The new specimens are from the upper Henson Gletscher Formation and the basal Kap Stanton Formation in Nyeboe Land, and they are from the *Ptychagnostus atavus* Zone and possibly basal *P. punctuosus* Zone.

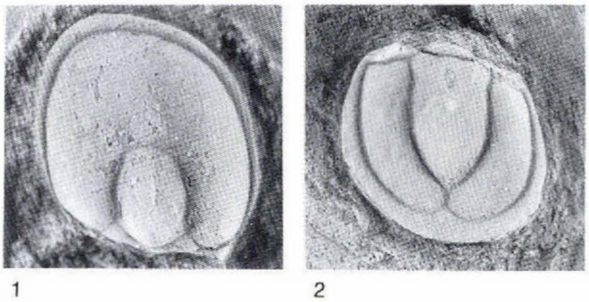


Fig. 17. *Hypagnostus parvifrons* (Linnarsson). 1, tectonically deformed cephalon, MGUH 21.385 from GGU 319789, × 8. 2, pygidium, MGUH 21.386 from GGU 319790, × 8.

Genus *Peronopsis* Hawle & Corda, 1847

Subjective junior synonyms include *Mesagnostus* Jaekel, 1909, *Euagnostus* Whitehouse, 1936, *Eoagnostus* Resser & Howell, 1938, *Archaeagnostus* Kobayashi, 1939, *Itagnostus* Öpik, 1979, *Svenax* Öpik 1979, *Axagnostus* Laurie, 1990; questionable synonyms include *Acadagnostus* Kobayashi, 1939 and *Micagnostus* Khajrullina *in* Repina *et al.*, 1975.

Type species. Battus integer Beyrich, 1845, p. 44.

Emended diagnosis. Genae anteriorly confluent. Glabella subcylindrical to slightly conical, rounded posteriorly, unequally divided by straight or nearly straight F3. Axial furrow may be incompletely effaced around anteroglabella. Basal lobes simple. Pygidium axiolobate and simplimarginate with ring furrows (F1, F2) variably developed. Posteroaxis ogival to lanceolate.

Remarks. More that a hundred species-group taxa having primitive agnostoid characters have been assigned to *Peronopsis* Hawle & Corda, 1847, including some of the oldest known agnostoids of late Early Cambrian age. Some species are based on large populations of well-preserved specimens that have been well documented. Many others, however, are based on one or a few specimens that commonly are incomplete, immature, poorly preserved, or otherwise inadequate for differential diagnosis. Since 1847, several *Peronopsis*-like genera have been proposed, but little attention has been given to phylogenetic relationships between them or to the taxonomic value of defining characters. In recent comments on the subject, Zhang & Jell (1987, p. 45) concluded that "until these genera are interpreted on an international basis and their morphological features found to be consistent it serves no purpose to distribute one or two species among these very closely related and typologically erected genera." I concur in principle with that conclusion.

Many species that have been assigned to *Peronopsis* seem to represent a plexus of gradational lineages. During more than three decades of investigating such agnostoids, I have from time to time attempted to differentiate and define early peronopsid lineages as a prelude to possible application of either available or new generic names. From these investigations, I have been unable to identify characters, or sets of characters, with which I have confidence in their value for differentiation of phylogenetic lineages. Therefore, I continue the common practice of assigning agnostoid species with primitive characters to *Peronopsis* in the broad sense.

Peronopsis, as here diagnosed, includes the oldest known agnostoids. These are characterised by small late-holaspid size, commonly a bipartite glabella, simple basal lobes, confluent genae, narrow border furrows on the cephalon and pygidium, a short, broad, unfurrowed pygidial axis with weak median node, and lack of spines. Some early species (e.g., *P. roddyi* and its probable synonyms *P. acrorhachis* and *P. primigenea;* compare Rasetti & Theokritoff, 1967, pp. 193–194, pl. 20, figs 1–22) show variable effacement of the axial furrow around the anteroglabella, and it is unclear whether this is a primitive or derived character. Such effacement also is variable in some later species (e.g., *P. opimus* Whitehouse; compare Robison *in* Jell & Robison, 1978, pp. 9–10, pl. 2, figs 1–6), but it became complete and stable as a holaspid character in some clades that have been designated by generic names (e.g., *Hypagnostus, Kormagnostus*).

Among evolutionary trends demonstrated by some later species of *Peronopsis* are increase in maximum holaspid size, lengthening of the pygidial axis, variable development of ring furrows (F1, F2) on the pygidium, enlargement of the median node to a tubercle on the pygidial M2, widening of cephalic and pygidial border furrows, and appearance of a pair of spines on the posterior pygidial border. Weak genal scrobiculae rarely appeared during late generic phylogeny. Early species generally lack constriction of the pygidial axis, whereas most later species have a constricted M2 ring. With M2 constriction, the associated posteroaxis is commonly ogival, but may become lanceolate. Most of these characters also vary during ontogeny, and character transformations are interpreted to be heterochronic in origin. It is these collective factors that make taxonomic subdivision of *Peronopsis* difficult.

In comparing the type species of *Peronopsis* and *Axagnostus* (*Peronopsis integra* and *Agnostus fallax*, respectively), differential characters cited by Laurie (1990, p. 318) include shape of the anteroglabella, size of basal lobes, convexity of the pygidial border, constriction of the pygidial M2, length of the pygidial axis, and shape of the posteroaxis. In my opinion, the morphological differences between these two taxa are minor and are comparable to those commonly encountered between two species of the same agnostoid genus. At this time, I see little advantage in recognising two genera, and therefore consider *Axagnostus* to be a junior synonym of *Peronopsis*.

Peronopsis is cosmopolitan and eurytopic in marine lithofacies. It has an observed stratigraphic range from the upper Lower Cambrian to the upper Middle Cambrian.

Peronopsis bulkurensis Pokrovskaya & Pegel *in* Egorova *et al.*, 1982

Fig. 18

Peronopsis bulkurensis Pokrovskaya & Pegel *in* Egorova *et al.*, 1982, p. 68, pl. 56, figs 11, 12

New material. Six cephala and 7 pygidia are in GGU 298975.

Remarks. The cephalon of *Peronopsis bulkurensis* is not very distinctive. The late holaspid pygidium, however, is as much as 50% wider than long and is characterised by a swollen axis with a straight articulating furrow, weakly developed ring furrows, moderate-sized median tubercle, tumid posteroaxis, wide border furrow, and paired border spines of moderate size. During holaspid ontogeny, the pygidial axis anisometrically became wider, longer and more tumid, and the postaxial median furrow decreased in relative length and became less well defined.

Specimens of *P. bulkurensis* closely resemble those of *P. lata* Shabanov *in* Savitsky *et al.* (1972, p. 65, pl. 7, figs 13, 14) and *P. recta* Pokrovskaya & Egorova *in* Savitsky *et al.* (1972, pp. 65–66, pl. 7, figs 9, 10). Differences between these species appear to be more taphonomic than genetic, and the names may be synonyms. Further investigation of Siberian material is needed in order to test this possibility.

Pygidia of *P. bulkurensis* somewhat resemble those of *P. fallax* but the posteroaxis is more tumid, the ring furrows are better developed, the postaxial median furrow is not effaced on larger holaspides, and the posterior border is narrower and not as flat.

Occurrence. Peronopsis bulkurensis has been previously reported from Siberia in the upper part of the *Ptychagnostus atavus* Zone. The new specimens are from the upper Henson Gletscher Formation of Nyeboe Land, and are also from the *Ptychagnostus atavus* Zone.

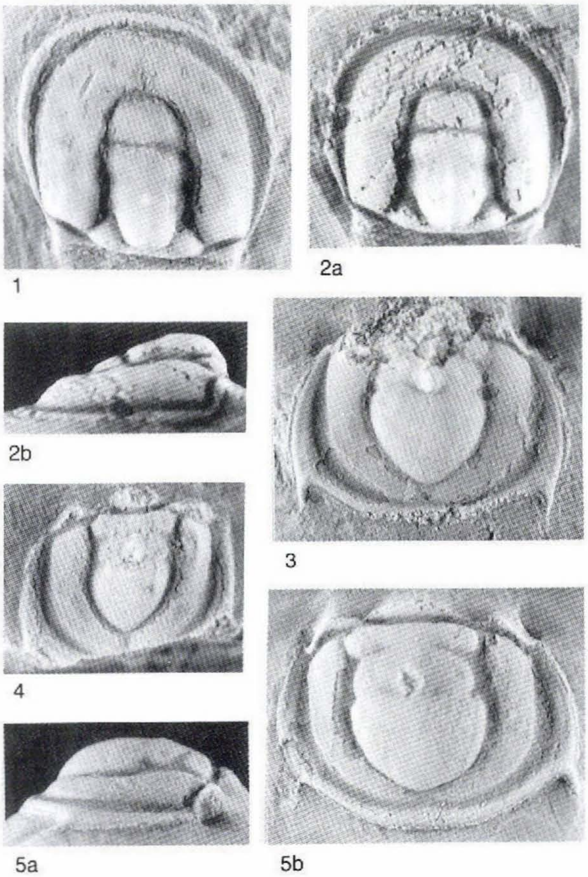


Fig. 18. *Peronopsis bulkurensis* Pokrovskaya & Pegel. All specimens from GGU 298975. 1, cephalon with weak scrobicular pits on the genae and partly exfoliated furrows, MGUH 21.387, × 8. 2a, b, partly exfoliated cephalon in dorsal and lateral views, MGUH 21.388, × 8. 3, 4, incomplete pygidia, MGUH 21.389 and 21.390, both × 8. 5, pygidium in lateral and dorsal views, MGUH 21.391, × 7.

Peronopsis fallax (Linnarsson, 1869)

Fig. 19.3, 4

New material. Six pygidia are in GGU 319789 and 319790. Cephala of *P. fallax* are probably present in these collections, but I have been unable to identify them with confidence, partly because of poor preservation, and partly because closely similar cephala of other species of *Peronopsis* are present in the same collections.

Remarks. The taxonomy of *P. fallax* has been previously reviewed (Robison, 1982, pp. 152–156). In a subsequent study by Laurie (1990), *fallax* was reassigned as the type species of a new genus *Axagnostus*, and the concept of the species was significantly restricted. Upon further review of this species, I concede that inclusion of some

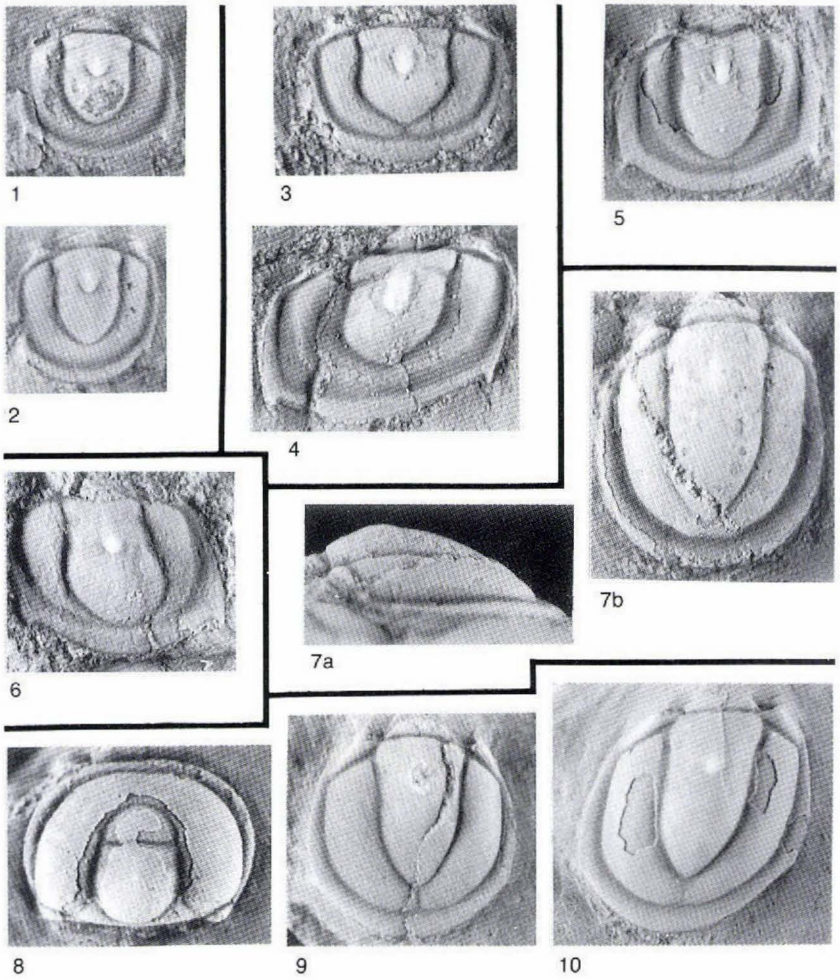


Fig. 19. Some species of *Peronopsis*.

1, 2, *Peronopsis ferox* (Tullberg); pygidia, MGUH 21.392 and 21.393 from GGU 298975, both × 10.

3, 4, *Peronopsis fallax* (Linnarsson), both from GGU 319790. 3, pygidium, MGUH 21.394, × 10. 4, pygidium, MGUH 21.395, × 7.

5, *Peronopsis* sp. 3; pygidium, MGUH 21.396 from GGU 301313, × 10.

6, *Peronopsis* sp. 2; latex cast of pygidium, MGUH 21.397 from GGU 319790, × 8.

7, *Peronopsis* sp. 1; lateral (a) and dorsal (b) views of pygidium, MGUH 21.398 from GGU 319789, × 8.

8–10, *Peronopsis interstricta* (White) from GGU 319790. 8, cephalon, MGUH 21.399, × 8. 9, 10, pygidia, MGUH 21.400 and 21.401, both × 6.

specimens in my synonymy list of 1982 may warrant reconsideration, primarily because of their poor preservation or inadequate illustration. Nevertheless, my concept of *fallax* remains essentially unchanged, and is based on greater intrapopulation variability than seems to be accepted by Laurie.

Specimens of *P. fallax* are rare in the new collections and are not well preserved.

Occurrence. The new specimens are from basal beds of the Kap Stanton Formation in Nyeboe Land, and are from the upper *Ptychagnostus atavus* Zone.

Peronopsis ferox (Tullberg, 1880)

Fig. 19.1, 2

New material. Two small holaspid pygidia of *P. ferox* are in GGU 298975. Cephala of this species also may be present, but if so I have been unable to confidently differentiate them from cephala of other species of *Peronopsis* in the collection.

Remarks. Specimens of *P. ferox* are common at some localities in the western United States. A description of these and a taxonomic review of the species are being prepared for separate publication. The new pygidia are assigned to the species because of the short axis, effaced ring furrows, confluent pleural fields of uniform breadth, and pair of small marginal spines (compare Westergård, 1946, p. 38, pl. 2, fig. 27, pl. 3, fig. 2; Robison, 1972a, pp. 242–243, fig. 2A-F; Öpik, 1979, pp. 54–55, pl. 4, figs 4–7). They resemble pygidia of *Agnostus lophotus* n. sp., but differ by having a more straight articulating furrow and a posterior border that narrows toward the marginal spines.

Occurrence. P. ferox is rare in one collection from the upper Henson Gletscher Formation in Nyeboe Land, and the collection is from the *Ptychagnostus atavus* Zone.

Peronopsis interstricta (White, 1874)

Fig. 19.8–10

Agnostus interstrictus White, 1874, p. 7

Peronopsis interstricta (White), Robison, 1964, p. 530 (synonymy to date), pl. 81, fig. 29, pl. 82, figs 1–15, 18; Robison, 1972a, pp. 244–245, fig. 4A-C; Gunther & Gunther, 1981, pl. 44, fig. B; Robison, 1982, pp. 156–157, pl. 6, pp. 9–11; Young & Ludvigsen, 1989, p. 11, pl. 1, figs 21–26, pl. 2, figs 1, 2; Robison, 1991, fig. 8.3

New material. More than 50 specimens, most tectonically deformed, are in GGU 319789 and 319790.

Remarks. The new specimens conform well with previous diagnoses (e.g., Robison, 1964, p. 530; Young & Ludvigsen, 1989, p. 11).

Specimens of *P. interstricta* from North America and Greenland closely resemble those of *P. opimus* (Whitehouse, 1936) from Australia, differing mainly in less effacement of the axial furrow around the anteroglabella, slightly more posterior placement of the glabellar node, and a shorter pygidial axis (compare Robison *in* Jell & Robison, 1978, p. 10). The chronostratigraphic range of *P. interstricta* encloses that of *P. opimus,* and it is possible that these minor differences may be phenotypic rather than genotypic. In the absence of a test for this hypothesis, however, I continue to recognise *P. opimus* as a separate species.

Occurrence. P. interstricta has been previously reported from the United States (Nevada, Utah) and Canada (western Newfoundland). In North Greenland, new specimens were collected from basal beds of the Kap Stanton Formation in Nyeboe Land. The composite observed species range is from the basal *Ptychagnostus gibbus* Zone into the *Ptychagnostus punctuosus* Zone. Associated agnostoids indicate that the Greenland specimens are from the upper *Ptychagnostus atavus* Zone.

Peronopsis cf. *pusilla* (Tullberg, 1880)

Fig. 20

Material. About 25 specimens are in GGU 298974, 298975, and 319790.

Remarks. Several specimens of *Peronopsis* from North Greenland closely resemble Swedish representatives of *P. pusilla* (e.g. Westergård, 1946, pp. 42–43, pl. 4, figs 12–18), a species characterised by weak genal scrobiculae, low relief of the anteroglabella, a short pygidial axis with effaced ring furrows, and a longer than usual postaxial median furrow. The new specimens differ, however, in having smooth genae, greater relief of the anteroglabella, and wider cephalic and pygidial borders. Although minor, these differences are stable in the small samples from North Greenland. Whether these are phenotypic or genotypic differences is an open question, and I therefore leave open the species assignment of these specimens.

Some of the specimens from Greenland are larger than any previously illustrated for *P. pusilla.* The entire population demonstrates ontogenetic elongation of the pygidial axis, correlative shortening and final effacement of the postaxial median furrow, and incipient development of a transverse sulcus on the posteroaxis (Fig. 20.4). In outline, the pygidium also grades from subcircular in small holaspides to subquadrate in large holaspides. The largest pygidium (Fig. 20.4) has fine radial ridges on the pleural fields.

Öpik (1979, pp. 64–65) reassigned *P. pusilla* as the type species of a new genus *Svenax.* For reasons stated in the remarks on *Peronopsis,* I consider *Svenax* to be a junior synonym.

Occurrence. Specimens are common in two collections

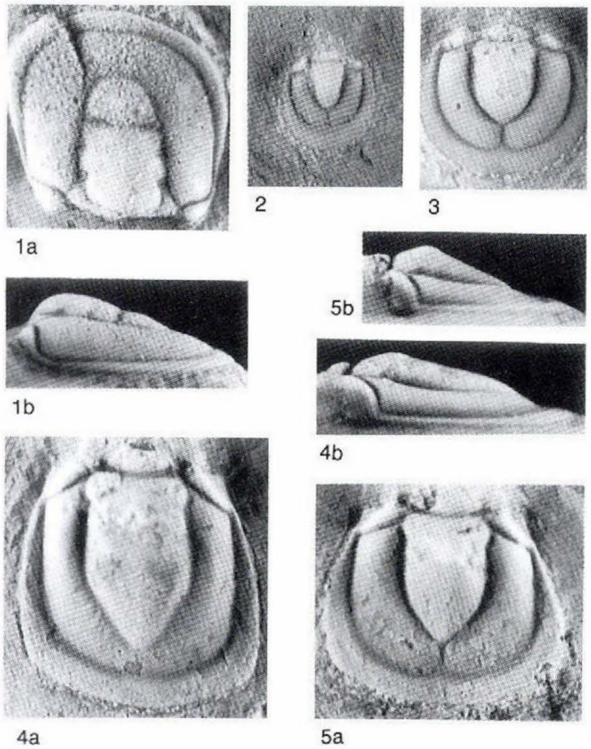


Fig. 20. *Peronopsis* cf. *pusilla* (Tullberg). All specimens from GGU 298975. 1a, b, cephalon in dorsal and lateral views, MGUH 21.402, × 7. 2, 3, smaller holaspid pygidia, MGUH 21.403 and 21.404, both × 10. 4, 5, larger holaspid pygidia in dorsal (a) and lateral (b) views, MGUH 21.405 and 21.406, both × 8.

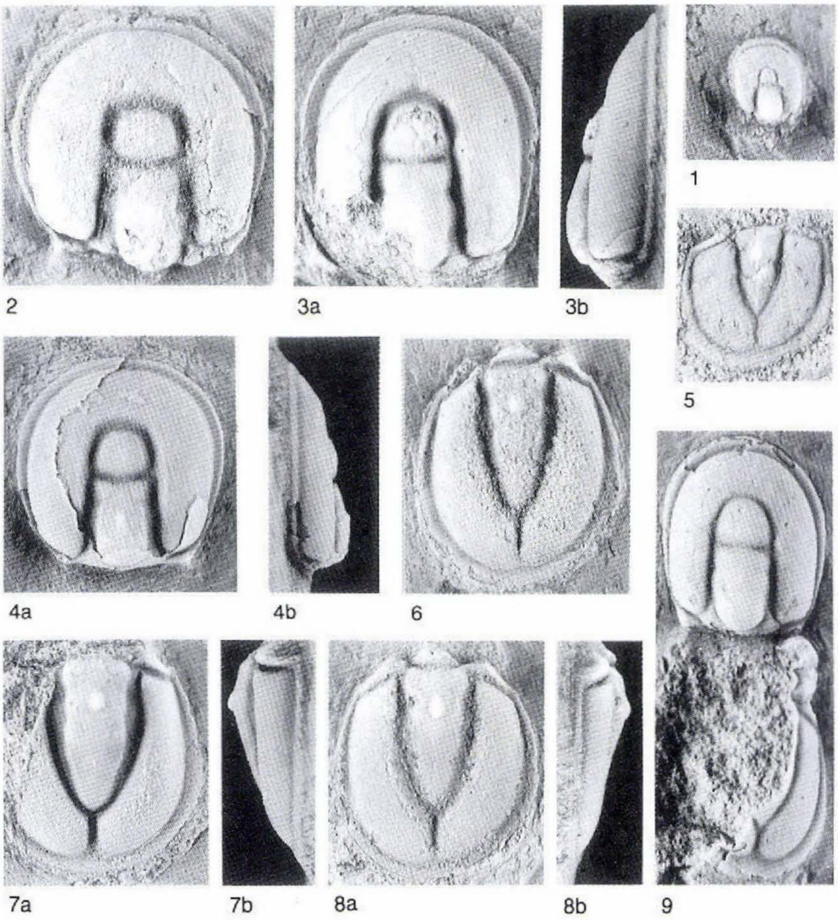


Fig. 21. *Peronopsis scutalis* (Hicks). 1, small holaspid cephalon, MGUH 21.407 from GGU 298969, × 10. 2, mostly exfoliated, large holaspid cephalon, MGUH 21.408 from GGU 298969, × 5. 3a, b, dorsal and lateral views of partly exfoliated cephalon showing posterior development of incipient preglabellar median furrow, MGUH 21.409 from GGU 298970, × 5. 4a, b, dorsal and lateral views of partly exfoliated cephalon having finely punctate genae, MGUH 21.410 from GGU 298969, × 5. 5, small holaspid pygidium, MGUH 21.411 from GGU 298969, × 8. 6, exfoliated pygidium, MGUH 21.412 from 298969, × 5. 7a, b, exfoliated, incomplete pygidium in dorsal and lateral views, MGUH 21.413 from GGU 298970, × 5. 8a, b, exfoliated pygidium in dorsal and lateral views, MGUH 21.414 from GGU 298969, × 5. 9, mostly testate but incomplete exoskeleton, MGUH 21.415 from GGU 310790, × 6.

from the upper Henson Gletscher Formation and one pygidium is in a collection from the basal Kap Stanton Formation, all from Nyeboe Land. All three collections are from the *Ptychagnostus atavus* Zone. For comparison, *Peronopsis pusilla* has been previously reported from Sweden, Norway, Denmark, and Australia where it has a composite observed stratigraphic range from the *P. atavus* Zone to the *P. punctuosus* Zone (Westergård, 1946, p. 43, Öpik, 1979, pp. 64–65). Howell (1925, pp. 37–38) also reported *Peronopsis* cf. *pusilla* and *Ptychagnostus punctuosus* in a faunal list for eastern Newfoundland, Canada.

Peronopsis scutalis (Hicks, 1872)
Fig. 21

New material. More than 100 specimens are in GGU 298969, 298970, 319789, and 319790.

Emended diagnosis. Peronopsis having narrow border furrows, moderately deep to deep axial furrow, and no border spines. Cephalon subcircular to subquadrate. Glabella slightly tapering toward anterior, length approximately two-thirds that of cephalon, F3 well defined; anteroglabella slightly wider than long, broadly rounded anteriorly; posteroglabella with median node near midlength. Pygidium subcircular to ovoid. Axis variable in length, with posterior end depressed; F1 and F2 mostly or entirely effaced; median tubercle on M2 small but prominent; posteroaxis lanceolate with secondary median node at about midlength. Postaxial median furrow deep.

Remarks. Peronopsis scutalis is used here in the broad sense of Westergård (1946, pp. 41–42) and Rushton (1979, pp. 50–51). The name is applied to a common group of *Peronopsis* in which length and terminal shape of the pygidial axis is variable. Several authors, including myself (Robison, 1988, p. 48), have attempted to taxonomically differentiate this group. After further study, partly based on new material, I now conclude that published information is an inadequate basis for meaningful taxonomic subdivision of the group. Further progress will probably require detailed analysis of type material of several taxa, most of which is not available to me at this time. Smaller holaspides from Greenland closely resemble the lectotype of *Agnostus exaratus tenuis* Illing, 1916, which was reillustrated as *Peronopsis scutalis tenuis* by Rushton (1979, fig. 3G).

Westergård (1946, p. 41) mentioned that most cephala and pygidia of *P. scutalis* in collections from Sweden are between 2 and 3 mm long, and shields 5 to 6 mm long are rare. In comparison, cephala and pygidia 5 to 6 mm long are common in new GGU collections from Greenland. These larger specimens usually have much deeper and stronger axial and postaxial median furrows than do smaller holaspides, especially those with a cephalon or pygidium less than about 3 mm long. Some accentuation of dorsal furrows on the larger holaspides, however, may be related to taphonomic compression in an argillaceous matrix. During holaspid ontogeny of Greenland specimens the posterior end of the pygidial axis changed from acutely pointed (Fig. 21.5) to sharply rounded (Fig. 21.7a). Larger holaspides also may have a shallow transverse sulcus on the posteroaxis.

Specimens that I previously assigned to *Peronopsis tenuis* (Robison, 1988, pp. 47–48, fig. 10.7, 8, 10–12)) are here reassigned to *P. scutalis* in the broad sense. Those preserved in grainstone have a secondary median node near the posterior end of the axis (Robison, 1988, fig. 10.10, 11), whereas new specimens preserved in argillaceous mudstone have a secondary node further forward on the axis (Fig. 21.7a). Whether or not these nodes are homologous and whether or not their positions are genotypically or phenotypically controlled are all unknown. Therefore, the position of such nodes is not here accorded taxonomic value.

Occurrence. Peronopsis scutalis is widespread in open-marine lithofacies that mostly seem to represent cool-water environments. It has a composite observed stratigraphic range from the *Ptychagnostus gibbus* to the *Lejopyge laevigata* zones. The new specimens are from the upper Henson Gletscher Formation and the basal Kap Stanton Formation, both in Nyeboe Land, and these specimens have an observed range from the *P. gibbus* Zone to the upper *Ptychagnostus atavus* Zone.

Peronopsis sp. 1

Fig. 19.7

Remarks. A single pygidium in GGU 319789 lacks spines and is characterised by an unusually long posteroaxis. It closely resembles a pygidium from the *Lejopyge laevigata* Zone of Sweden that Westergård (1946, p. 43, pl. 3, fig. 16) illustrated as *Peronopsis* cf. *insignis* (Wallerius), but differs by having a more elongate and less distinct axial node, a less angular lateral profile, and by lacking paired muscle scars. The new specimen is from basal beds of the Kap Stanton Formation of Nyeboe Land, and is from the upper *Ptychagnostus atavus* Zone.

Peronopsis sp. 2

Fig. 19.6

Remarks. A single undetermined pygidium of *Peronopsis* is in GGU 319790 from the upper *Ptychagnostus atavus* Zone in basal beds of the Kap Stanton Formation, Nyeboe Land. Its lateral margins diverge slightly toward the posterior and it has a long axis that extends to the posterior border. Ring furrows are nearly effaced and the median node is strong and elongate. The posteroaxis is laterally expanded and has a broadly angular posterior margin. The border furrow is moderately wide, the posterior border is medially expanded, and a pair of border spines are of moderate size. The taxonomic affinities of this specimen within *Peronopsis* are unclear. It superficially resembles the pygidium of *Iniospheniscus incanus* Öpik, but its axis is narrower, its lateral margins diverge rather than converge toward the posterior, and its border spines are larger.

Peronopsis sp. 3

Fig. 19.5

Remarks. A small, single, undetermined pygidium of *Peronopsis* is in GGU 301313 from the *Lejopyge laevigata* Zone in basal beds of the Kap Stanton Formation, Peary Land. It is characterised by an elongate, subcylindrical axis that extends almost to the posterior border furrow. The median node is carinate, ring furrows are very weak on the exfoliated surface, and a secondary median node is on a long posteroaxis about one-third of its length from the back margin. The border furrow is wide, the lateral and posterior borders are subequal in width except anterolaterally where they narrow, pleural fields are narrow but confluent behind the axis, and two border spines are small. This pygidium resembles that of smaller holaspides of *Peronopsis bulkurensis,* but it has a longer axis, lacks a postaxial median furrow, and has a secondary median node. It also resembles the pygidium of *Peronopsis* sp. 2 but its posteroaxis is not laterally swollen and its exterior border is more uniform in width.

Family Ptychagnostidae Kobayashi, 1939

Remarks. The family diagnosis of Robison (1984) is followed here. Further phylogenetic analysis during this study, in part based on new material, has identified two ptychagnostid lineages showing parallel evolution. Each lineage commenced with a furrowed species and each evolved highly effaced, homeomorphic species. The available names *Lejopyge* Hawle & Corda, 1847 and *Pseudophalacroma* Pokrovskaya, 1958 are here applied to these lineages. The diagnosis of each genus is emended accordingly (see below).

In previous discussion of *Lejopyge*, Öpik (1979, pp. 158–159) concluded that a high degree of effacement evolved twice in separate lineages within the genus, and that one lineage maintained its continuity in the species of *Pseudophalacroma.* Although the two lineages discussed by Öpik share some species with the two lineages identified here, our conclusions differ significantly on the source of each lineage and its species content (see remarks below on *Lejopyge* and *Pseudophalacroma*).

The Ptychagnostidae, after generic emendations that follow, includes *Ptychagnostus, Goniagnostus, Lejopyge, Myrmecomimus, Pseudophalacroma* and *Tomagnostus. Tomagnostella* is questionably assigned to the family.

Genus *Lejopyge* Hawle & Corda, 1847

Lejopyge Hawle & Corda, 1847, p. 51; Kobayashi, 1937, pp. 437–447; Kobayashi, 1939, pp. 131–132; Lermontova, 1940, p. 130; Westergård, 1946, p. 87; Pokrovskaya, 1958, pp. 72–76; Howell *in* Harrington et al., 1959, p. 178; Pokrovskaya *in* Chernysheva, 1960, p. 60; Öpik, 1961, p. 85; Robison, 1964, p. 521; Palmer, 1968, p. 27; Daily & Jago, 1975, pp. 527–550; Jago, 1976, p. 12; Öpik, 1979, pp. 157–159; Robison, 1984, pp. 36–37; Robison, 1988, p. 48; Laurie, 1989, pp. 186–188; Shergold *et al.*, 1990, p. 40

Miagnostus Jaekel, 1909, p. 401

Onymagnostus Öpik, 1979, pp. 107–108; Robison, 1984, pp. 50–51; Laurie, 1988, p. 187; Shergold *et al.*, 1990, p. 41

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

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

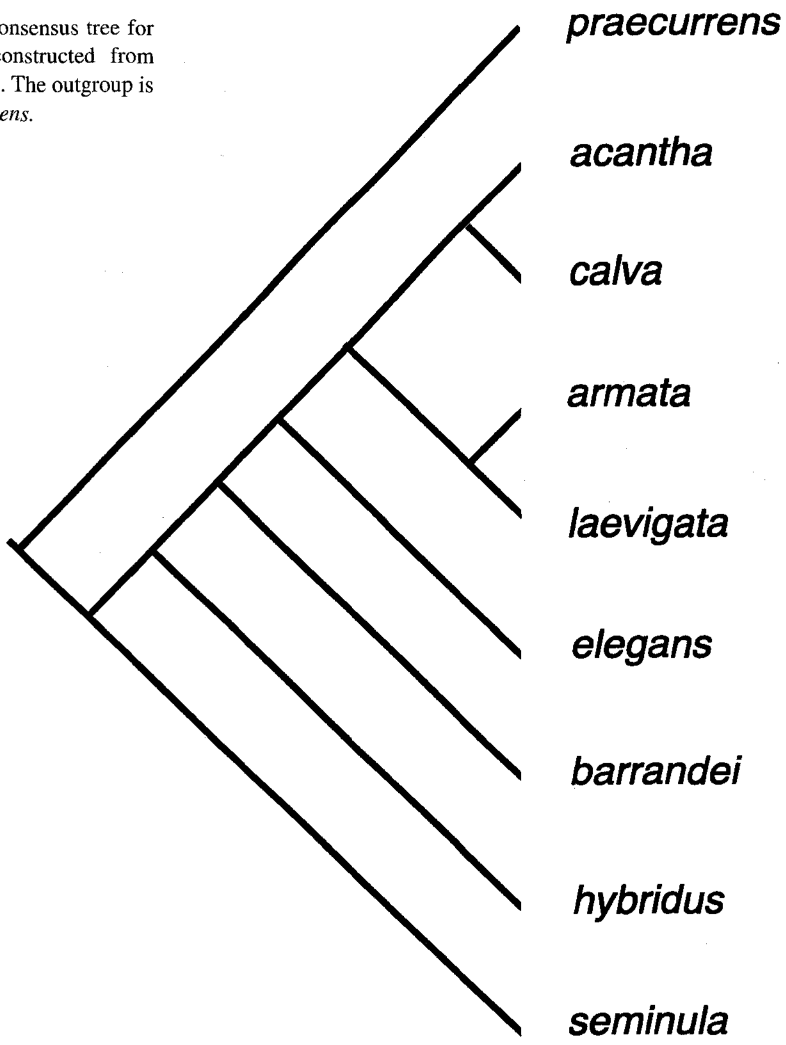
Emended diagnosis. Ptychagnostidae with furrows on acrolobes well developed to mostly effaced. Glabella elongate, slightly and irregularly tapered, rounded to bluntly pointed anteriorly. Basal lobes slightly elongate to simple. Cephalic border of variable width in furrowed species, becoming very narrow in highly effaced species. Genae smooth to weakly scrobiculate. Pygidial axis long to moderately long; M2 hexagonal; posteroaxis commonly ogival on furrowed species, becoming almost lanceolate with near effacement of axial furrow. Postaxial median furrow becoming effaced and pygidial pleurae becoming confluent during ontogeny, usually by early stages of holaspid period. Pygidial border fairly uniform in width laterally and posteriorly, narrowing at anterolateral corners; moderately wide in furrowed species, becoming narrow in effaced species. Spine development variable and iterative on posterior cephalic border, thorax, and posterior pygidial border.

Remarks. After further phylogenetic analysis, the concept of *Lejopyge* Hawle & Corda, 1847 is here emended from previous discussion (Robison, 1984, pp. 36–37). It also is broadened to include species that have not been previously assigned to the genus, and the generic synonymy is significantly modified.

Prior to 1979, authors assigned to *Lejopyge* only species having advanced effacement of furrows on the acrolobes. In his monograph on Swedish agnostoids, Westergård (1946, p. 87) summarised the taxonomic history of *Lejopyge*, and concluded (p. 75) that "*Ptychagnostus* (*Tr.*) *elegans, elegans laevissimus,* and *Lejopyge laevigata* constitute an evolutional series with very small intervals." In 1979, Öpik (p. 158) noted his acceptance of Westergård's phyletic concept, but assigned all three of the taxa cited by Westergård to *Lejopyge.* To the beginning of the phyletic series, and to the genus *Lejopyge*, he also reassigned *Agnostus lundgreni* Tullberg, 1880 and *A. lundgreni* var. *nana* Grönwall, 1902, which are furrowed taxa. Following Öpik, I (Robison, 1984, p. 37) accepted *lundgreni* as the ancestral species of *Lejopyge*, and further suggested (p. 46) that *L. lundgreni* probably originated from a lineage containing *Ptychagnostus intermedius.* Laurie (1989, p. 176) also included *lundgreni* in *Lejopyge*, but re-evaluated some morphology to support an alternative suggestion "that an origin for *Lejopyge* lies somewhere within *Onymagnostus*."

As a test of the phylogeny suggested by Laurie, I have analysed the characters of several species of *Lejopyge* and *Onymagnostus* using PAUP (Swofford, 1990). *Ptychagnostus praecurrens* was selected as the outgroup because it is the oldest known species of the Ptychagnostidae (Robison, 1978, p. 2) and it has character states that are inferred to be primitive for the family. It was found that most species of *Lejopyge* cluster closely with those of *Onymagnostus*, but they do not cluster closely with *lundgreni,* which supports Laurie's suggestion regarding the source of *Lejopyge.* Further phylogenetic analysis of species (Fig. 22 and Table 2), based in part on new and well-preserved specimens from North Greenland, has indicated that *Agnostus barrandei* Hicks, 1872 and *Agnostus elegans* Tullberg, 1880 fill intermediate positions in a multi-character morphological gradient leading from *Agnostus hybridus* Brøgger, 1878, the type species of *Onymagnostus*, to *Battus laevigata* Dalman, 1828, the type species of *Lejopyge.* In an exhaustive search in which all characters were equally weighted, five parsimony trees were discovered. The majority-rule consensus tree (Fig. 22) has the same arrangement of species as one of the

Fig. 22. Majority-rule consensus tree for species of *Lejopyge* constructed from character data in Table 2. The outgroup is *Ptychagnostus praecurrens.*



parsimony trees. The morphological changes between each of the analysed species are judged to be taxonomically trivial. Also, it is clear from Fig. 22 that *Onymagnostus*, as recognised by previous authors, is paraphyletic. For these reasons, I now propose the suppression of *Onymagnostus* as a subjective junior synonym of *Lejopyge*.

As emended, *Lejopyge* includes *L. laevigata* (Dalman, 1828), *L. armata* (Linnarsson, 1869), *L. barrandei* (Hicks, 1872), *L. hybridus* (Brøgger, 1878), *L. elegans* (Tullberg, 1880), *L. seminula* (Whitehouse, 1939), *L. calva* Robison, 1964, and *L. acantha* Robison 1984. The inferred phylogenetic relationship of these species is shown by Fig. 22. With further evaluation, other previously named species may also warrant assignment to *Lejopyge*.

The described morphological differences between *L. seminula* and *Onymagnostus semiermis* Öpik, 1979 are comparable to the variation observed within large populations of *L. hybridus,* and I therefore further propose the suppression of *semiermis* as a subjective junior synonym of *L. seminula.* The geographic source and age of the holotype of *L. seminula* are questionable (Robison, 1982, pp. 148–150).

Some species that were previously assigned to *Lejopyge*, including *A. lundgreni* and *Lejopyge rigbyi* Robison, 1984, are here reassigned to *Pseudophalacroma* (see below).

Lejopyge, as emended, is interpreted to be a monophyletic (holophyletic) genus that commences with *L. seminula,* an inferred descendent of *Ptychagnostus praecurrens.* Some species of *Lejopyge* retain a primitive furrowed condition and others show variable effacement of acrolobe features. Furrowed species are characterised by an elongate axial lobe. The glabella has a minor and irregular taper. A median node is anterior from the mid-

Table 2. Characters, character states and data matrix for Ptychagnostus praecurrens *and* Lejopyge *used to construct the cladogram*

Late holaspid characters, character states, and data matrix for *Ptychagnostus praecurrens* and eight species of *Lejopyge*, which were used to construct the cladogram in Fig. 22. Characters not preceded by an asterisk and scored '0' represent the ancestral state, and the same characters scored '1,' '2,' '3,' or '4' represent derived states coded as additive transformations. For characters preceded by an asterisk (*), the character states are unordered. A question mark (?) indicates missing data. If multistate characters are present in a species, the most common state is scored in the data matrix.

*1. Cephalic border spines: absent (0) or present (1).
2. Preglabellar median furrow: present (0) or effaced (1).
*3. Axial furrow of cephalon: fully developed (0), uniformly weak (1), effaced anterior of F3 (2), effaced anterior of F2 (3), or effaced anterior of basal lobes (4).
*4. Basal lobes: slightly elongate (0), simple (1), or elongate (2).
5. Cephalic F3: fully developed (0), weak (1), or effaced (2).
*6. Median node of posteroglabella: behind midpoint (0), at midpoint (1), or in front of midpoint (2).
*7. Pygidial border spines: absent (0), incipient (1), or fully developed (2).
8. Postaxial median furrow: present (0) or effaced (1).
*9. Separation of pygidial axis and posterior border furrow: moderate (0), narrow (1), or wide (2).
*10. Axial furrow of pygidium: fully developed (0), weak (1), effaced behind F2 (2), or effaced behind F1 (3).
11. Pygidial F1: fully developed (0), weak (1), or effaced (2).
12. Pygidial F2: fully developed (0), weak (1), or effaced (2).
*13. Pygidial M2 with median: node (0), tubercle (1), or spine (2).
14. Posteroaxis: ogival (0) or lanceolate (1).

Species	Character													
	1	2	3	4	5	6	7	8	9	10	11	12	13	14
P. praecurrens	0	0	0	0	0	0	0	0	0	0	0	0	0	0
L. acantha	1	1	4	1	2	?	0	1	?	3	2	2	0	?
L. armata	1	1	3	1	2	0	2	1	0	2	2	2	0	?
L. barrandei	0	1	2	1	1	2	0	1	2	1	1	1	1	0
L. calva	0	1	4	1	2	?	0	1	?	3	2	2	0	?
L. elegans	0	1	1	1	1	1	0	1	0	1	1	1	0	1
L. hybridus	0	0	0	1	0	2	0	1	0	0	0	0	1	0
L. laevigata	0	1	3	1	2	0	0	1	?	2	2	2	0	?
L. seminula	0	0	0	0	0	2	1	1	1	0	0	0	1	0

point of the posteroglabella in furrowed species, but its more posterior position in some effaced species suggests either migration of a single node during phylogeny or possible suppression of the original node and development of a latent, more posterior node (compare Robison, 1984, p. 17). Basal lobes are slightly elongate in *L. seminula,* the earliest species of *Lejopyge*, but are mostly simple in later species of the genus. Width of the cephalic border is fairly uniform within species, but varies during phylogeny, ranging from moderate in furrowed species to very narrow in some effaced species. The pygidial axis is ogival in species with a well-developed axial furrow, but approaches a lanceolate condition with near effacement of that furrow in *L. elegans* (e.g., Westergård, 1946, pl. 10, figs 14, 19). It is also important to note that taphonomic compression and deformation of furrowed specimens in argillaceous matrix has commonly resulted in deepening of some furrows (especially the axial furrow), narrowing of the axial lobe, and deformation of the axial tip to a pointed, pseudolanceolate condition. On the pygidial axis of furrowed species the second ring is characteristically hexagonal and has a large posteromedian tubercle that deeply embays the second ring furrow (F2). With intermediate effacement of the acrolobe, as in *L. barrandei,* a smaller node may be superimposed on the median tubercle (see Fig. 23.3), or the F2 and the primary tubercle may disappear, leaving only the smaller secondary node (see Fig. 23.8). Width of the pygidial border is usually moderate and fairly uniform, but may narrow slightly in species with advanced effacement of the acrolobe.

Lejopyge and *Pseudophalacroma*, as emended, have overlapping geographic and stratigraphic ranges. Early, furrowed species of *Lejopyge* clearly differ from early, furrowed species of *Pseudophalacroma* by having a longer axial lobe, a less tapered glabella, a median node that is anterior rather than posterior from the midpoint of the posteroglabella, a larger tubercle on the pygidial M2, usually no postaxial median furrow on late holaspides, and a pygidial border of more uniform width. Advanced effacement of the acrolobes in late species of both *Lejopyge* and *Pseudophalacroma* makes generic identification difficult. Nevertheless, late species of *Lejopyge* differ from late species of *Pseudophalacroma* by having a pygidial border that is sagittally narrower and which remains more uniform in width.

Some partially effaced agnostoids closely similar to *Lejopyge barrandei* have been assigned to *Cotalagnostus.* Review of literature on *Cotalagnostus*, as well as some type material, suggests that polyphyletic species have been assigned to the genus. It also appears likely that the only two illustrated syntypes of the type species, *Agnostus lens* Grönwall, 1902, represent two species. Therefore, to stabilise nomenclature and taxonomic concepts, I here select the illustrated syntype pygidium (Grönwall, 1902, pl. 1, fig. 9) to be the lectotype of *A. lens.* That lectotype appears to represent a peronopsid, whereas the illustrated syntype cephalon, except for size, is virtually indistinguishable from the only illustrated syntype cephalon of *Agnostus altus* Grönwall (1902, pl.

1, fig. 3), which is here considered to be a junior synonym of *Lejopyge barrandei*.

Lejopyge, as emended, is widely distributed in open-marine lithofacies and has an observed stratigraphic range from the lower *Ptychagnostus gibbus* Zone to at least the top of the *L. laevigata* Zone.

Without an opportunity to observe type material of *Phoidagnostus* Whitehouse, 1936, I (Robison, 1984, pp. 36–37) previously accepted Öpik's (1961, pp. 54, 86; 1967, p. 76) conclusion that *Phoidagnostus* is a synonym of *Lejopyge*. After re-examination of the holotype of *P. limbatus*, the type species of *Phoidagnostus*, Laurie (1989, pp. 187–188) concluded that *Phoidagnostus* is not a synonym of *Lejopyge*. Subsequently, Shergold *et al.* (1990, p. 56, fig. 18.5) gave a diagnosis of *Phoidagnostus*, assigning it under 'Familae Incertae Sedis,' and they published the first photograph clearly illustrating the holotype of *P. limbatus*. That holotype is a cephalon and incomplete thorax of an effaced agnostoid that appears to be taphonomically deformed. In my opinion, its poor preservation and lack of diagnostic characters preclude adequate comparison with other effaced agnostoid taxa. Therefore, I now consider *Phoidagnostus* to be an unrecognisable genus.

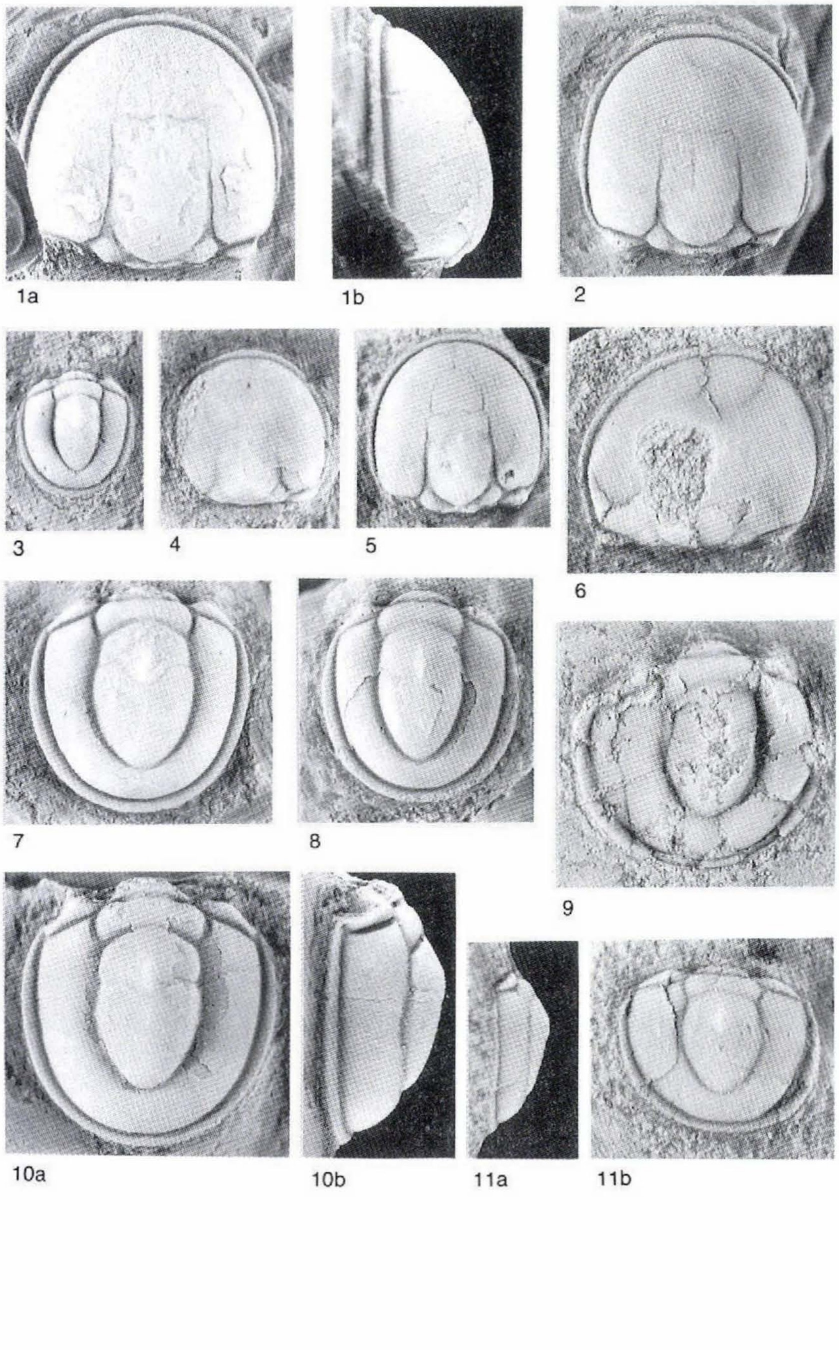


Fig. 23. *Lejopyge barrandei* (Hicks). All specimens preserved with original convexity in calcareous matrix of GGU 298970, unless stated otherwise. 1a, b, large, mostly exfoliated cephalon in dorsal and lateral views, MGUH 21.416, × 5. 2, cephalon, MGUH 21.417, × 6. 3, pygidium, MGUH 21.418, × 8. 4, 6, cephala partially flattened in argillaceous matrix, MGUH 21.419 and 21.420 from GGU 298969, × 8 and × 6. 5, cephalon, MGUH 21.421, × 8. 7, pygidium, MGUH 21.422, × 6. 8, partly exfoliated pygidium having densely spaced, fine punctae in test, MGUH 21.423, × 6. 9, pygidium flattened in argillaceous matrix, MGUH 21.424 from GGU 298969, × 6. 10a, b, large, partly exfoliated pygidium in dorsal and lateral views, MGUH 21.425, × 5. 11a, b, pygidium, slightly flattened in argillaceous matrix, in lateral and dorsal views, MGUH 21.426 from GGU 298969, × 8.

Lejopyge barrandei (Hicks, 1872)

Fig. 23

Agnostus barrandei Hicks, 1872, p. 176, pl. 5, figs 5, 6; Lake, 1906, p. 13, pl. 2, fig. 2; Illing, 1916, p. 413, pl. 30, figs 13, 14; Lake, 1946, p. 338

Agnostus laevigatus var. *terranovicus* Matthew, 1896, pp. 233–234, pl. 17, figs 1a, 1b

Agnostus laevigatus var. *ciceroides* Matthew, 1896, p. 234, pl. 17, figs 3a, 3b

?*Agnostus laevigatus* var. *mammilla* Matthew, 1896 (in part), p. 234, pl. 17, fig. 2a (not 2b) [see Hutchinson, 1962, p. 86]

Agnostus altus Grönwall, 1902, pp. 58–59, pl. 1, figs 3, 4; Lake, 1906, pp. 12–13, pl. 2, fig. 1; Illing, 1916, p. 412, pl. 30, figs 9, 10

?*Agnostus lens* Grönwall, 1902 (in part), pp. 65–66, pl. 1, fig. 8 (not 9)

Cotalagnostus altus (Grönwall), Whitehouse, 1936, p. 93; Kobayashi, 1939, p. 129; Pokrovskaya *in* Chernysheva, 1960, pl. 1, fig. 30

Cotalagnostus barrandei (Hicks), Whitehouse, 1936, p. 93; Kobayashi, 1939, p. 129

Cotalagnostus illingi Kobayashi, 1939, p. 129

Cotalagnostus ciceroides (Matthew), Kobayashi, 1939, p. 129

Cotalagnostus mammillata (Matthew), Kobayashi, 1939, p. 129

Cotalagnostus terranovicus (Matthew), Kobayashi, 1939, p. 129

Ptychagnostus convexus Westergård, 1946, pp. 73–74, pl. 10, figs 5–10

Ptychagnostus ciceroides (Matthew), Hutchinson, 1962 (in part); 85–86, pl. 9, figs 20–22 (?not 23), pl. 10, figs 2–8 (?not 1); Poulsen, 1969, pp. 5–6, fig. 5a, ?5b

Ptychagnostus barrandei (Hicks), Rushton, 1979, p. 54, fig. 5A-B; Morris, 1988, p. 195

Onymagnostus altus (Grönwall), Öpik, 1979, p. 107

Onymagnostus ciceroides (Matthew), Öpik, 1979, p. 107; Robison, 1984, p. 51; Morris, 1988, p. 155

Onymagnostus convexus (Westergård), Öpik, 1979, p. 107

not *Triplagnostus convexus* Westergård; Egorova, Pegel & Chernysheva *in* Egorova *et al.*, 1982, p. 65, pl. 2, figs 5, 7 [? = *Pseudophalacroma lundgreni* (Tullberg)]

Cotalagnostus aff. *altus* (Grönwall); Egorova, Pegel & Chernysheva *in* Egorova *et al.*, 1982, p. 73, pl. 8, figs 3, 8

Onymagnostus pseudomundus Xiang & Zhang, 1985, p. 76, pl. 16, figs 12, 13

Lectotype. Specimen figured by Hicks (1872, pl. 5, fig. 5) and Lake (1906, pl. 2, fig. 2), selected by Rushton (1979, p. 54).

New material. More than a hundred specimens are in GGU 298969, 298970, 298974, 298975, 319789, and 319790.

Emended diagnosis. Lejopyge with variable effacement of features on acrolobes. Cephalon and pygidium semicircular, highly convex, nonspinose. Axial furrow of cephalon weakening anteriorly, shallow to nearly effaced laterally, indistinct or effaced around anteroglabella; transglabellar furrow (F3) weak to effaced. Posteroglabella broad, subparallel sided; median node anterior from midpoint. Basal lobes simple. Genae usually smooth; preglabellar median furrow effaced. Cephalic border narrow. Axial furrow of pygidium variable in depth, but distinct, ranging from moderately deep to almost effaced. Pygidial axis relatively short for genus, well rounded posteriorly on later holaspides; F1 moderate to shallow in depth, bowed anteriorly; F2 shallow to effaced, indented by median tubercle of M2 that may have superimposed node. Postaxial median furrow usually absent on holaspides. Pygidial border moderate to narrow in width.

Remarks. L. barrandei is a species of *Lejopyge* characterised by intermediate and variable effacement of furrows on the acrolobes. The degree of effacement increased during ontogeny, especially on the cephalon, which has been noted in populations from Sweden (Westergård, 1946, p. 73) and Newfoundland (Hutchinson, 1962, p. 85), and is clearly evident in populations from North Greenland. Also, the degree of effacement may be influenced by taphonomy, seemingly being enhanced by compression in argillaceous matrix (Fig. 23.4, 6, 9, 11). Such variability has contributed to a proliferation of taxonomic names from widespread localities (see synonymy).

Some specimens of *L. barrandei* and *Cotalagnostus lens* are similarly effaced, making their identification difficult. Usually, however, *L. barrandei* has narrower cephalic and pygidial borders of more uniform width, lacks a postaxial median furrow, and the pygidial F1 is usually evident and clearly deeper than the F2.

Occurrence. L. barrandei, as emended, has been reported from England, Wales, Canada (eastern Newfoundland), Greenland (Nyeboe Land), Denmark, Sweden, Russia (Siberia), and China (Xinjiang). The new material is from the upper Henson Gletscher and the basal Kap Stanton formations of Nyeboe Land. The composite observed stratigraphic range of the species is throughout most of the *Ptychagnostus atavus* and *Ptychagnostus punctuosus* zones.

Lejopyge calva Robison, 1964

Fig. 24

Remarks. A single effaced cephalon and a fragmentary, associated pygidium in collection GGU 301311 are assigned to *L. calva* (compare Robison, 1984, pp. 40–42, fig. 23.1–8). Although the posterior border on the pygidium is slightly wider than usual for this species, the cephalic features, including degree of effacement of fur-

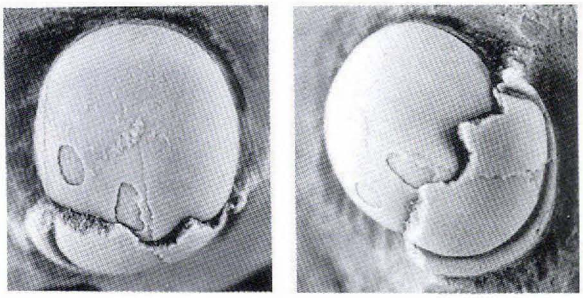

1a 1b

Fig. 24. *Lejopyge calva* Robison. Slightly exfoliated cephalon (1a) and associated, fragmentary pygidium (1b), MGUH 21.427 from GGU 301311, × 10.

rows on the acrolobe, are characteristic of the species. The specimen is from near the base of the Kap Stanton Formation in Peary Land and is associated with a fauna of the lower *Lejopyge laevigata* Zone. This is the first report of *L. calva* from Greenland.

Laurie (1989) recently reviewed the species of *Lejopyge* in Australia, and he reassigned a few Australian specimens to *L. calva*. Most or all of those specimens, in my opinion, represent *Pseudophalacroma* as emended here rather than *Lejopyge*. Specimens of *Lejopyge praecox* Öpik, 1979 were independently and almost simultaneously reassigned to *Lejopyge dubium* (Whitehouse) by Robison (1988, p. 49) and to *L. calva* by Laurie (1989, p. 189). Based on the wide pygidial border of *praecox*, as well as other features, I still consider it to be a synonym of *dubium*, but *dubium* is here reassigned to *Pseudophalacroma* (see below).

Lejopyge hybridus (Brøgger, 1878)

Fig. 25.1, 2, 3?, 4?

New material. More than 30 specimens are in GGU 319790 and 6 questionably assigned specimens are in GGU 298969 and 301311.

Remarks. The species diagnosis of Robison (1984, pp. 51–54) is followed here, although the species is reassigned from *Onymagnostus* to *Lejopyge*. A synonymy and taxonomic discussion were included with that diagnosis. Laurie (1988, pp. 187–189) subsequently published a shorter but essentially similar diagnosis under the name *Onymagnostus hybridus*. In referring to my 1984 list of synonyms, Laurie noted some assignments that he stated to be incorrect. Of those, I agree that one specimen from Utah, which was previously illustrated as *Ptychagnostus hybridus* (Robison, 1964, pl. 79, fig. 11), is a representative of *Doryagnostus* (see remarks on *Doryagnostus*). Laurie further noted that the holotype of *Triplagnostus formosus* Pokrovskaya & Khajrullina *in* Repina *et al.* (1975, pl. 9, fig. 9), which in 1984 I reassigned to *hybridus*, probably also belongs to *Doryagnostus*. I concur with that probability, but am unable to make a firm judgment from available illustrations. The inclusion of *T. formosus* in Laurie's (1988, p. 187) list of synonyms of *O. hybridus* indicates a generic assignment that is contrary to that made in his remarks (p. 188–189).

A few Australian taxa that I listed in 1984 as synonyms of *Onymagnostus hybridus* were reassigned by Laurie (1988, p. 189) as synonyms of *O. mundus* Öpik, 1979. Laurie stated that *O. mundus* and taxa that he synonymised with it "are all very similar but differ from *O.*

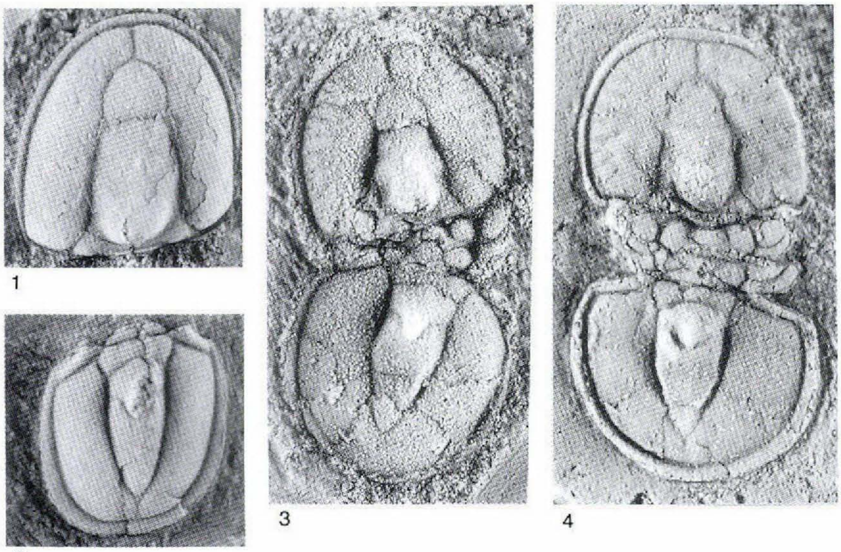

1 2 3 4

Fig. 25. *Lejopyge hybridus* (Brøgger). 1, partly exfoliated and tectonically deformed cephalon, MGUH 21.428 from GGU 319790, × 8. 2, partially flattened pygidium with axis possibly narrowed by compression, MGUH 21.429 from GGU 319790, × 10. 3, questionably assigned, deformed exoskeleton, MGUH 21.430 from GGU 3013ll, × 6. 4, questionably assigned, flattened exoskeleton, MGUH 21.431 from GGU 298969, × 8.

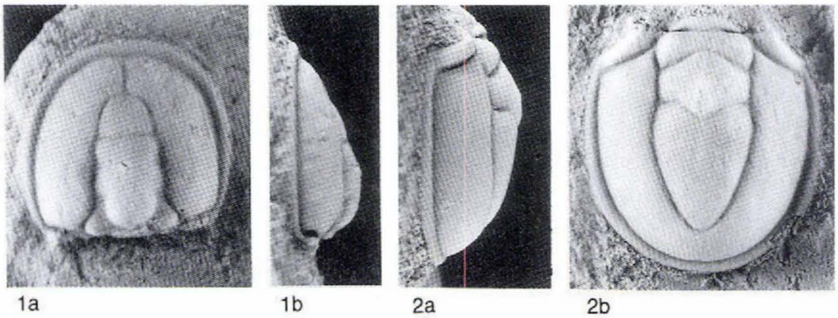


Fig. 26. *Lejopyge* cf. *seminula* (Whitehouse) from GGU 298970. 1a, b, cephalon in dorsal and lateral views, MGUH 21.432, × 10. 2a, b, pygidium in lateral and dorsal views, MGUH 21.433, × 6.

hybridus ... in having very weakly impressed axial furrows and in having a narrower, less bluntly pointed anterior glabellar lobe." In large populations of *hybridus* that I have observed, depth of the axial furrow is variable, and the average depth varies from population to population. The shape of the anterior glabella also is variable. With regard to anterior glabellar shape, Laurie (1988, pp. 187, 189) used identical wording, "rounded to obtusely pointed," in describing that character in his diagnoses of both *O. hybridus* and *O. mundus*. Therefore, I continue to suppress *O. mundus* as a subjective junior synonym of *L. hybridus*.

The new specimens from Greenland provide no new information about morphology of the species.

Occurrence. L. hybridus is a common, widely distributed species in open-marine lithofacies. Several new specimens are from basal beds of the Kap Stanton Formation in Nyeboe Land (e.g., Fig. 25.1, 2), one questionably assigned specimen is from the basal Kap Stanton Formation in Peary Land (Fig. 25.3), and a few other questionably assigned specimens are from the upper Henson Gletscher Formation in Nyeboe Land (e.g., Fig. 25.4). The assigned specimens are from the *Ptychagnostus atavus* Zone. The questionably assigned specimens are mostly from the *Ptychagnostus atavus* Zone, but one is from the lower *Lejopyge laevigata* Zone.

Lejopyge cf. *seminula* (Whitehouse, 1939)

Fig. 26

Remarks. Eleven specimens in GGU 298970 have morphological characters that appear to be transitional between those of *Lejopyge seminula* and *L. hybridus* (compare Robison, 1984, pp. 51–55, figs 30–32). They resemble specimens of *L. seminula* by having slightly elongate basal lobes, but length of the axial lobe is more similar to that of *L. hybridus*. Therefore, their assignment to a species is problematic.

The new specimens are from the middle Henson Gletscher Formation of Nyeboe Land, and they probably are from the uppermost *Ptychagnostus gibbus* Zone. This biostratigraphic occurrence is intermediate between ranges previously observed for *L. seminula* and *L. hybridus* (Robison, 1984, pp. 54–55).

Genus *Pseudophalacroma* Pokrovskaya, 1958

Pseudophalacroma Pokrovskaya, 1958, p. 79; Öpik, 1961, pp. 90–92; Öpik, 1967, p. 77; Öpik, 1979, p. 163; Qiu *et al.*, 1983, p. 38; Lu & Lin, 1989, pp. 100–101, 218–219

Type species. Pseudophalacroma crebra Pokrovskaya, 1958, pp. 79–80; by original designation [= *P. dubium* (Whitehouse, 1936), see Robison, 1988, p. 49].

Emended diagnosis. Ptychagnostidae with furrows of acrolobes well developed to mostly effaced. Glabella short, moderately and rather evenly tapered, anteriorly acute. Basal lobes simple. Genae usually smooth. Cephalic border narrow to thread-like. Pygidial axis short, F1 deeper than F2; posteroaxis lanceolate to slightly ogival. Postaxial median furrow present if posterior axial furrow is not effaced. Pygidial border moderate to narrow in width; widest medially, gradually narrowing toward anterior corners. Spines may be present on cephalon, thorax, and pygidial axis; not observed on pygidial border.

Remarks. Parts of the preceding diagnosis necessarily pertain only to species that lack much effacement of furrows on the acrolobes. Such species first appear in the *Ptychagnostus punctuosus* Zone, and are present only in the lower stratigraphic range of *Pseudophalacroma* as emended.

Pseudophalacroma seems to be a monophyletic (holophyletic) genus that commenced with *P. lundgreni*. The origin of *P. lundgreni* within the Ptychagnostidae remains unclear, but it possibly arose from *Ptychagnostus intermedius* (see Robison, 1984, 46, fig. 6). Other species, as in *Lejopyge*, may retain the original furrowed condition or may show variable effacement of acrolobe features. Furrowed species are characterised by a relatively short axial lobe. The glabella tapers to an acute point, and a median node is posterior from the posteroglabellar midpoint. A prominent postaxial median furrow separates the pleural lobes on such furrowed species as *P. lundgreni* and *P. rigbyi,* and a vestige is evident on some exfoliated internal moulds of effaced species (Öpik, 1979, pl. 65, figs 1, 2; pl. 67, fig. 3; Robison, 1988, fig. 11.2). Characters that differentiate species of *Pseudophalacroma* and *Lejopyge* are discussed above in remarks on *Lejopyge.*

Species here included in *Pseudophalacroma* are *P. dubium* (Whitehouse, 1936), *P. lundgreni* (Tullberg, 1880), *P. multifora* (Öpik, 1979), *P. ovalis* (Yang, 1982), and *P. rigbyi* (Robison, 1984). *Pseudophalacroma triangularis* Ju *in* Zhang, 1983 and *P. breviovata* Ju *in* Zhang, 1983 are here considered to be junior synonyms of *P. ovalis.* The genus has an observed stratigraphic range from near the base of the *Ptychagnostus punctuosus* Zone to near the top of the *Lejopyge laevigata* Zone. It is widely distributed in open-oceanic lithofacies.

Dong (1990, p. 318, pl. 3, fig. 12) illustrated an agnostoid pygidium from western Hunan, China, as *Pseudophalacroma triangularis* Ju, and applied the same name to a new zone in upper Middle Cambrian strata of that region. With regard to the synonymy cited above, the zone named by Dong now should be called the *Pseudophalacroma ovalis* Zone. According to Song (1989, fig. 7), the Chinese stratigraphic interval containing *P. ovalis* questionably correlates with the *Ptychagnostus punctuosus* Zone as used in other parts of the world.

Although new specimens of *Pseudophalacroma* are not described here, an emended generic diagnosis is included for comparison with the emended diagnosis of *Lejopyge,* given above. Specimens from the Holm Dal Formation in North Greenland that were previously assigned (Robison, 1988, pp. 48–49, fig. 11.1–4) to *Lejopyge dubium* (Whitehouse) are here reassigned as *Pseudophalacroma dubium.*

Genus *Ptychagnostus* Jaekel, 1909

Type species. Agnostus punctuosus Angelin, 1851, p. 8.

Remarks. The generic diagnosis and description of *Ptychagnostus* by Robison (1984, pp. 12–13) are followed here. More restricted diagnoses of *Ptychagnostus* have been published by Laurie (1988, pp. 171–172) and Shergold *et al.* (1990, p. 39), who reassigned some species to five other genera or subgenera (*Triplagnostus* Howell 1935c, *Pentagnostus* Lermontova, 1940, *Acidusus* Öpik, 1979, *Aotagnostus* Öpik, 1979, and *Zeteagnostus* Öpik, 1979) that I continue to regard as junior synonyms of *Ptychagnostus.* My reasons for this synonymy remain unchanged from those expressed in 1984.

Shergold & Laurie (1991) have petitioned the *Interna tional Commission on Zoological Nomenclature* to use its plenary powers to conserve the name *Ptychagnostus.*

Ptychagnostus affinis (Brøgger, 1878)

Figs 10.5; 27.1, 2

New material. Two cephala and 2 pygidia are in GGU 319789 and 319790.

Remarks. The emended diagnosis of *P. affinis* by Robison (1984, pp. 16–17) is followed here. Laurie (1988, pp. 172–176) subsequently discussed the species and made corrections to its synonymy, with which I concur. The new specimens are all fragmentary.

Occurrence. The geographic and stratigraphic distributions of *P. affinis* were reviewed by Robison (1984, p. 17). With a correction by Laurie (1988), the species is no longer known from Alaska.

The new specimens are the first representatives of *P. affinis* to be reported from Greenland. All are from basal beds of the Kap Stanton Formation in Nyeboe Land, and are from the upper *Ptychagnostus atavus* Zone.

Ptychagnostus atavus (Tullberg, 1880)

Fig. 27.5, 6

New material. Two cephala and 2 pygidia are in GGU 319790.

Remarks. The emended diagnosis of *P. atavus* by Robison (1984, pp. 18–21) is followed here. A similar diagnosis was subsequently published by Laurie (1988, p. 180), but he reassigned the species to *Acidusus.* I agree with Westergård (1946, p. 68) that the species *atavus, affinis* and *punctuosus* "constitute a fairly continuous evolutional series," and like Westergård I assign them all to *Ptychagnostus. P. affinis* primarily differs from *P. atavus* by the more anterior position of the median node on the glabella, a weaker tubercle on the pygidial M2, and development of weak granulation on the pleural fields. In my opinion, these are characters that are appropriate for defining species, but not genera. Moreover, difference in position of the glabellar node may represent differential expression of latent nodes rather than evolutionary migration of one node (see Robison, 1984, p. 17).

Occurrence. P. atavus is a common, widely distributed species in open-oceanic lithofacies. The new specimens

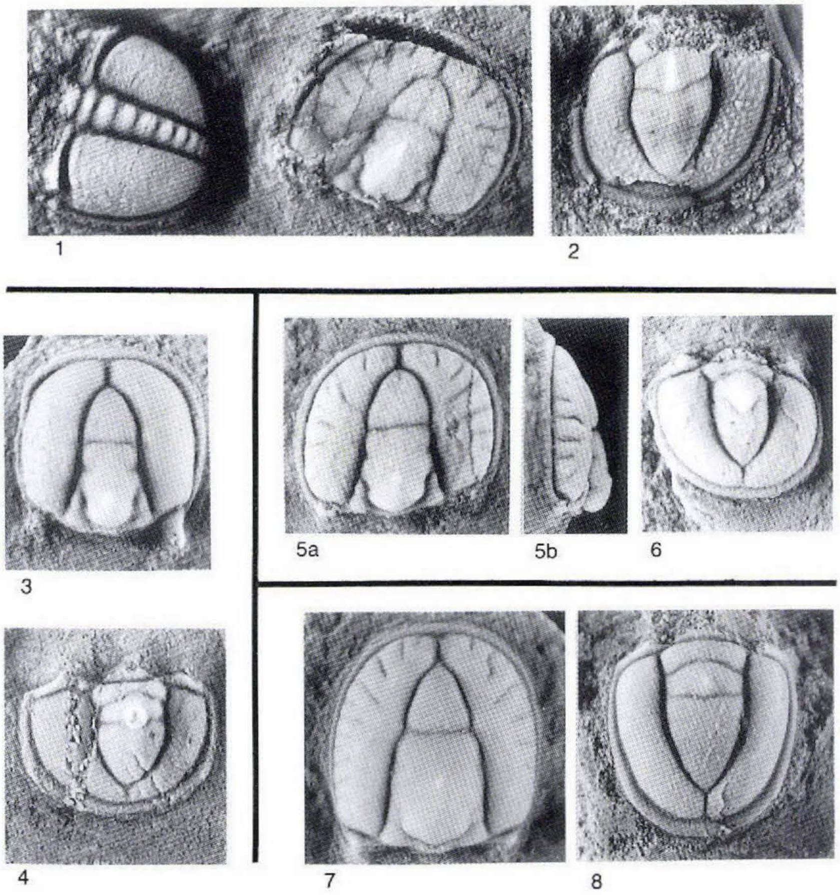


Fig. 27. Some species of *Ptychagnostus*.

1, 2, *Ptychagnostus affinis* (Brøgger). 1, damaged cephalon (right), MGUH 21.434, associated with pygidium of *Eodiscus scanicus* (Linnarsson), MGUH 21.303, from GGU 319789, × 12. 2, fragmentary pygidium, MGUH 21.435 from GGU 319790, × 10.

3, 4, *Ptychagnostus gibbus* (Linnarsson), both from GGU 298970. 3, cephalon, MGUH 21.436, × 12. 4, damaged pygidium, MGUH 21.437, × 10.

5, 6. *Ptychagnostus atavus* (Tullberg), both from GGU 319790. 5a, b, cephalon in dorsal and lateral views, MGUH 21.438, × 12. 6, pygidium, MGUH 21.439, × 12.

7, 8, *Ptychagnostus intermedius* (Tullberg), both from GGU 298970. 7, cephalon, MGUH 21.440, × 10. 8, pygidium, MGUH 21.441, × 10.

are the first to be reported from Greenland. All are from basal beds of the Kap Stanton Formation in Nyeboe Land, and are from the upper *Ptychagnostus atavus* Zone.

Ptychagnostus gibbus (Linnarsson, 1869)

Fig. 27.3, 4

New material. More than 10 disarticulated specimens are in GGU 298970.

Remarks. The diagnosis of *P. gibbus* by Robison (1984, pp. 22–24) is followed here. Additional synonyms, mostly from Australia, were listed and discussed by Laurie (1988, pp. 196–198). He, however, assigned the species to *Triplagnostus*, which I consider to be a junior synonym of *Ptychagnostus*.

The new specimens from Greenland mostly are small and not well preserved.

Occurrence. The new specimens of *P. gibbus* are from the middle Henson Gletscher Formation of Nyeboe Land, and are from the *P. gibbus* Zone.

Ptychagnostus intermedius (Tullberg, 1880)

Fig. 27.7, 8

New material. More than 20 disarticulated specimens are in GGU 298970.

Remarks. Laurie (1988, p. 178) has suggested that Tullberg's syntypes of *Agnostus intermedius* may be conspecific with *Ptychagnostus affinis* (Brøgger, 1878), and he (1988, p. 172) listed *A. intermedius* as a questionable synonym of *P. affinis*. He also reassigned to *Zeteagnostus scarifatus* (Öpik, 1979) specimens that I (Robison, 1982, 1984) previously assigned to *Ptychagnostus intermedius* (Brøgger). Laurie further suggested that *Z. scarifatus* may be a junior synonym of *Ptychagnostus sinicus* Lu 1957. These suggestions warrant additional investigation, but pending their verification, I continue to follow an earlier diagnosis (Robison, 1984, pp. 25–28) of *P. intermedius*.

The new specimens from Greenland fall well within the range of variation shown by other populations of *P. intermedius*.

Occurrence. The new specimens of *P. intermedius* are from the middle Henson Gletscher Formation of Nyeboe Land, and are from the *Ptychagnostus gibbus* Zone.

Genus *Tomagnostus* Howell, 1935c

Tomagnostus Howell, 1935c, p. 15; Whitehouse, 1936, p. 90; Harrington, 1938, pp. 149, 154; Kobayashi, 1939, pp. 149–150; Westergård, 1946, pp. 31, 58; Pokrovskaya, 1958, pp. 20–23; Howell *in* Harrington *et al.*, 1959, p. O175; Pokrovskaya *in* Chernysheva, 1960, p. 57; Rushton, 1979, pp. 54–55; Shergold *et al.*, 1990, p. 41

Type species. Agnostus fissus Linnarsson, 1879, p. 23.

Emended diagnosis. Ptychagnostidae with furrowed acrolobes. Glabella slightly to moderately tapered; anteroglabella usually having frontal sulcus; posteroglabella with median node or carina, F1 and F2 variably developed. Basal lobes slightly elongate, poorly defined anteriorly, and indenting glabella. Preglabellar median furrow weakening anteriorly or effaced. Genae having scrobiculae or irregular pits, or both. Cephalic border narrow. Pygidial axis having hexagonal M2; posteroaxis sulcate. Postaxial median furrow present or absent in middle and late holaspid stages. Pygidial border narrow, rarely collared.
Remarks. Tomagnostus has been variously assigned to the Agnostidae, Diplagnostidae, Peronopsidae, and Ptychagnostidae (see Rushton, 1979, p. 55; Shergold *et al.*, 1990, p. 41). Based on all characters, but with emphasis on those of the axial lobe, I concur with Shergold *et al.* (1990) in assigning *Tomagnostus* to the Ptychagnostidae. Comparative morphology suggests that early species of *Tomagnostus* are most closely related to early species of the ptychagnostid *Lejopyge*, as emended above. Details of cladogenesis, however, remain obscure.

Species here included in *Tomagnostus* are *T. fissus* (Linnarsson, 1879), *T. perrugatus* (Grönwall, 1902), *T. corrugatus* (Illing, 1916), *T. gracilis* (Illing, 1916), *T. bothrus* n. sp., and questionably *T. sibiricus* Pokrovskaya & Egorova *in* Savitsky et al., 1972. *Tomagnostus tchateriensis* Kryskov *in* Borovikov & Kryskov, 1963 was reassigned to *Innitagnostus* by Öpik (1967, p. 98), but *Innitagnostus* is here considered to be a junior synonym of *Micragnostus* (see remarks on *Agnostus*). *Tomagnostus clarus* Egorova & Pokrovskaya (*in* Egorova *et al.*, 1982) is reassigned to *Schismagnostus* n. gen. (see below).

Although *Tomagnostus* is a widespread genus, its distribution suggests that it may have been mostly or entirely adapted to cool-water habitats, but ranging in depth from shallow to deep. The genus has an observed stratigraphic range from the *Ptychagnostus gibbus* Zone to the *Ptychagnostus atavus* Zone, and questionably into the basal *Ptychagnostus punctuosus* Zone.

Tomagnostus bothrus n. sp.

Fig. 28.1–5, 7, 6?, 8?

Etymology. Greek *bothros*, pit; referring to the many scrobicular pits on the genae.

Holotype. Cephalon (Fig. 28.4a, b), MGUH 21.445 from GGU 298970.

Material. Six cephala and 2 questionably assigned pygidia are in GGU 298969 and 298970.

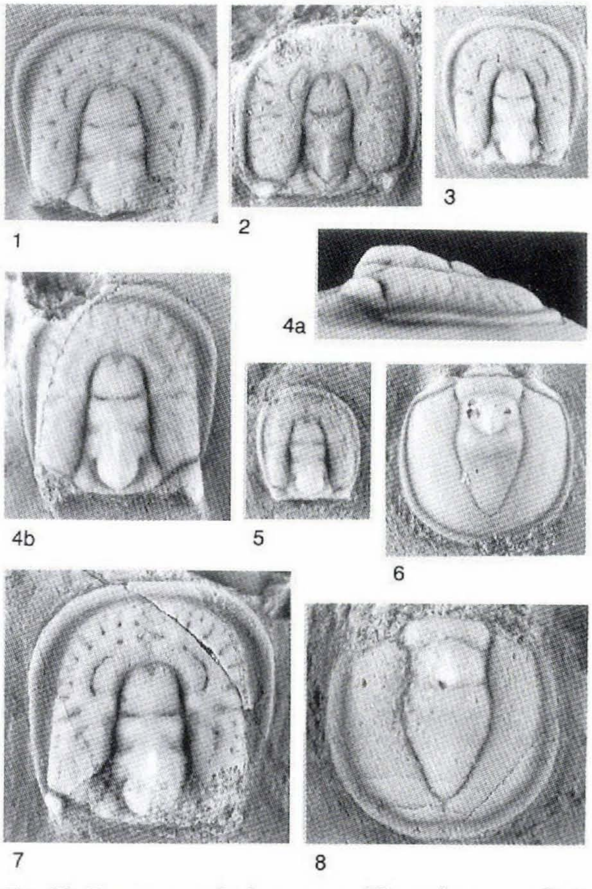


Fig. 28. *Tomagnostus bothrus* n. sp. All specimens are from GGU 298970, unless otherwise stated. 1, cephalon, MGUH 21.442, × 8. 2, cephalon, MGUH 21.443 from GGU 298969, × 8. 3, cephalon, MGUH 21.444, × 8. 4, holotype cephalon in lateral and dorsal views, MGUH 21.445, × 8. 5, small holaspid cephalon, MGUH 21.446, × 10. 6, questionably assigned pygidium, MGUH 21.447 from GGU 298969, × 8. 7, large holaspid cephalon, MGUH 21.448, × 7. 8, questionably assigned pygidium, MGUH 21.449, × 7.

Diagnosis. Tomagnostus with moderate convexity. Cephalon having narrow glabella, many scrobicular pits on genae, and posterolateral border spines. Questionably assigned pygidium with elliptical tubercle that is most tumid posteriorly, and with postaxial median furrow throughout holaspid period.

Description. Cephalon subquadrate. Glabella only slightly tapered; transverse furrow (F3) slightly bowed posteriorly, shallow medially, deep laterally. Anteroglabella semicircular to subtriangular, with moderately developed frontal sulcus. Posteroglabella having relatively well-developed F1 and F2 furrows; posterior end strongly rounded, distinctly constricted between basal lobes; median node subcentral, near front of M2, and may be connected to occipital band by thread-like median ridge. Preglabellar median furrow effaced except for weak posterior vestige. Genae with many scrobicular pits, some outlining pair of uninterrupted, arcuate regions on anterior genae; pits on inside of arcuate regions usually coalesced into pair of arcuate grooves opposite front of glabella. Border narrow, with pair of short, stout, posterolateral spines on larger holaspides.

Thorax unknown.

Questionably assigned pygidium subquadrate to subcircular. M2 having elliptical tubercle that is low and poorly defined anteriorly. Posteroaxis long and ogival. Postaxial median furrow present in late holaspid stage. Border narrow and nonspinose.

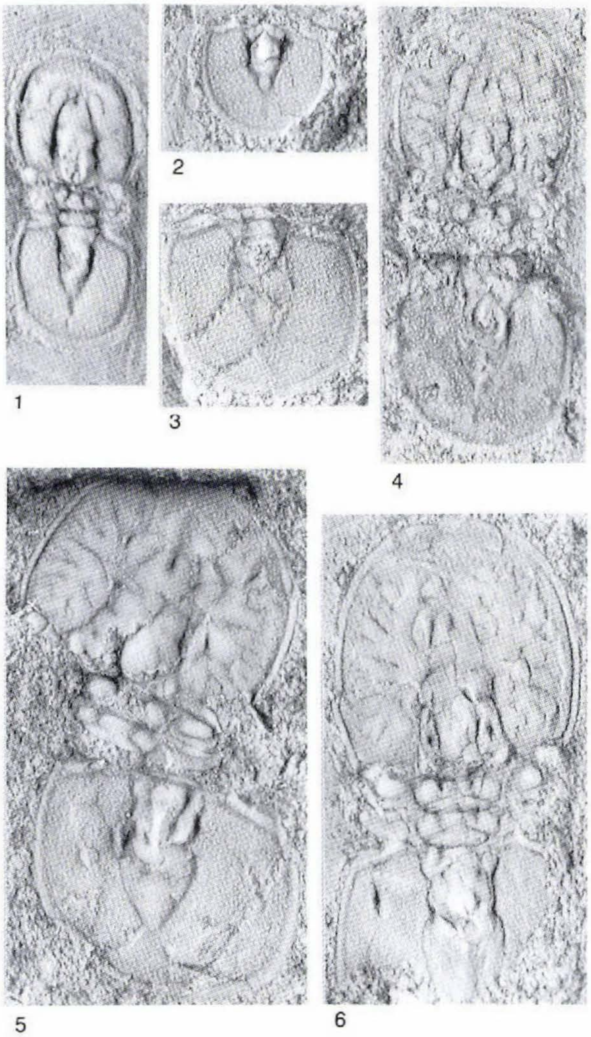


Fig. 29. *Tomagnostus corrugatus* (Illing). All specimens from GGU 298969. 1, small holaspid, MGUH 21.450, × 10. 2, pygidium, MGUH 21.451, × 8. 3, pygidium with tiny incipient spine on right-posterolateral margin. MGUH 21.452, × 8. 4–6, flattened dorsal exoskeletons, MGUH 21.453–21.455, all × 8.

Remarks. T. bothrus differs from all previously described species of *Tomagnostus* by having a pair of cephalic border spines. Two pygidia, which are questionably assigned to this species, have characteristic features of the genus except for retention of a postaxial median furrow in late ontogenetic stages.

The cephalon of *T. bothrus* further differs from that of *T. fissus* by having a narrower glabella and the genal prosopon is predominantly pits rather than grooves. The questionably assigned pygidia of *T. bothrus* differ from those of *T. fissus* by having a more pointed and better defined axial tip.

Larger holaspid cephala of *T. bothrus* resemble those of *Schismagnostus plicatus* n. gen. & n. sp. in general axial structure, but differ by the presence of a frontal sulcus, the F3 is nearly straight rather than bowed posteriorly, and the M1 is more constricted between the basal lobes. Other differences are the presence of border spines, longer basal lobes, and a different style of genal scrobiculae in *T. bothrus*. In axial shape, the questionably assigned pygidia of *T. bothrus* resemble those of *Ptychagnostus affinis* and *P. punctuosus*, but in low-incident light they show no evidence of surface granulation, which characterises the latter species.

Occurrence. The few specimens of *T. bothrus* are from the upper Henson Gletscher Formation in Nyeboe Land, and are from both the *Ptychagnostus gibbus* and *Ptychagnostus atavus* zones.

Tomagnostus corrugatus (Illing, 1916)

Fig. 29

Agnostus corrugatus Illing, 1916, pp. 409–410, pl. 29, figs 4, ?5, 6–9

Tomagnostus corrugatus (Illing), Kobayashi, 1939, p. 149; Pokrovskaya, 1958, pp. 27–30, pl. 2, figs 1–4; Rushton, 1979, p. 56, figs 6A-B, 7D-E

Tomagnostus deformis Pokrovskaya; Egorova, Pegel & Chernysheva *in* Egorova *et al.*, 1982 (in part), pl. 8, fig. 9; (not pl. 5, fig. 5; ?not pl. 12, fig. 13)

New material. More than 15 specimens, most flattened and poorly preserved, are in GGU 298969.

Emended diagnosis. Tomagnostus having thin exoskeleton of low convexity. Cephalon with moderately tapering glabella and well-developed genal scrobiculae. Pygidium having short and narrow axis, densely granular pleural fields, and may have pair of incipient marginal spines.

Remarks. All recorded specimens of *T. corrugatus* are preserved in fine-grained matrix and show evidence of taphonomic compression. Compared with associated agnostoids, the new specimens from Greenland are significantly more flattened and seem to have had a thinner exoskeleton. A paucity of taphonomically produced wrinkles, however, suggests that low convexity of the exoskeleton, and especially the pygidium, is a primary character.

Occurrence. T. corrugatus has been previously reported from the *Ptychagnostus atavus* Zone of England and Russia (Siberia). The new specimens are from the upper Henson Gletscher Formation in Nyeboe Land, and also are from the *P. atavus* Zone.

Tomagnostus fissus (Linnarsson, 1879)

Fig. 30

Agnostus fissus Linnarsson, 1879, p. 23, pl. 2, fig. 34; Tullberg, 1880, 16, pl. 1, fig. 3a-d; Linnarsson, 1883, p. 31; Matthew, 1896, pp. 230–231; Lake, 1906, pp. 3–4, pl. 1, figs 1–3; Illing, 1916, pp. 406–407, pl. 28, figs 6–8; Nicholas, 1916, p. 452

Agnostus fissus trifissus Matthew, 1896, pp. 231–232, pl. 16, fig. 10

?*Agnostus fissus* var. *perrugatus* Grönwall, Illing, 1916, p. 407, pl. 28, fig. 9

Tomagnostus fissus (Linnarsson), Howell, 1935c, p. 15, figs 9, 10; Kobayashi, 1939, p. 149; Westergård, 1946, pp. 58–59, pl. 7, figs 21–29, pl. 16, fig. 8; Pokrovskaya, 1958, pp. 23–27, pl. 1, figs 1–11; Howell *in* Harrington *et al.*, 1959, fig. 114.4; Pokrovskaya *in* Chernysheva, 1960, pl. 1, fig. 3; Hutchinson, 1962, pp. 76–77, pl. 7, figs 1–5; Egorova *et al.*, 1976, p. 59, pl. 37, figs 2–4, 11, 13, pl. 38, fig. 11, pl. 55, fig. 4; Rushton, 1979, fig. 7A-C; Egorova, Pegel & Chernysheva *in* Egorova *et al.*, 1982, p. 59, pl. 3, figs 1–4, pl. 4, fig. 1, pl. 6, fig. 6, pl. 8, figs 4–7, pl. 9, fig. 5, pl. 51, figs 7, 8; Kindle, 1982, pl. 1.2, figs 6, 10; Morris, 1988, p. 229; Shergold *et al.*, 1990, fig. 12.6a, b; Samson *et al.*, 1990, p. 1467, fig. 5C-E

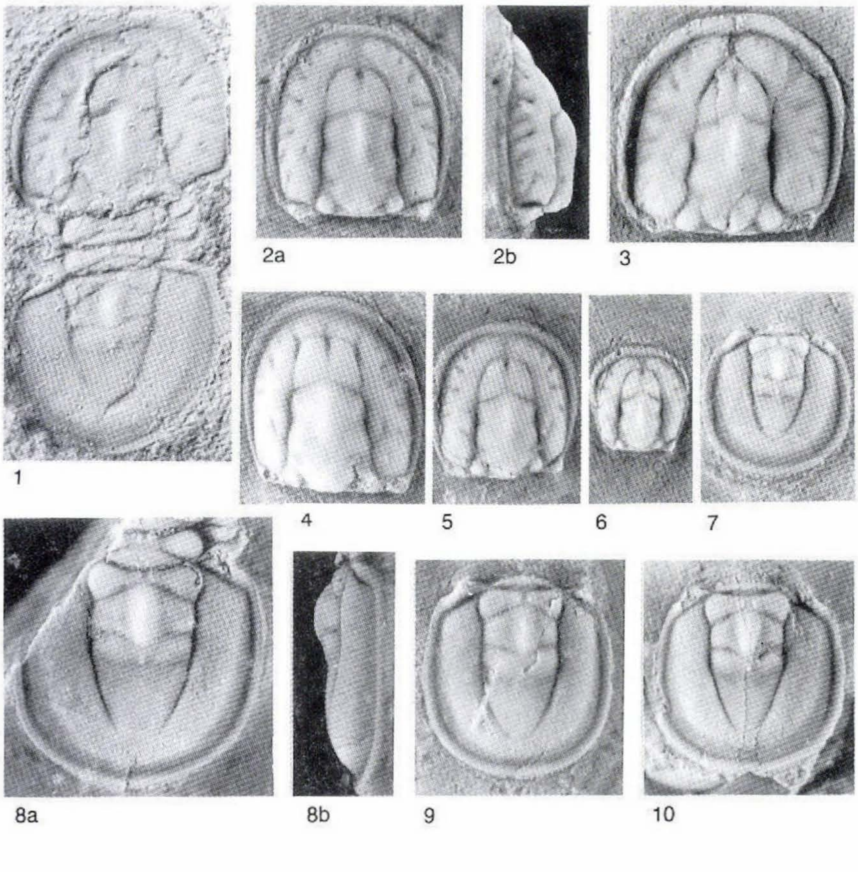


Fig. 30. *Tomagnostus fissus* (Linnarsson). All specimens from GGU 298970, unless otherwise stated, and all × 8. 1, latex cast of partially flattened exoskeleton, MGUH 21.456. 2a, b, dorsal and lateral views of cephalon, MGUH 21.457. 3, large holaspid cephalon, MGUH 21.458. 4, cephalon with pattern of genal scrobiculae similar to that described for *Tomagnostus fissus trifissus* (Matthew), MGUH 21.459 from GGU 298975. 5, 6, smaller holaspid cephala, MGUH 21.460 and 21.461. 7, pygidium, MGUH 21.462. 8a, b, incomplete, large holaspid pygidium in dorsal and lateral views, MGUH 21.463. 9, 10, pygidia, MGUH 21.464 and 21.465.

Tomagnostus fissus trifissus (Matthew), Kobayashi, 1939, pp. 149–150

New material. More than a hundred specimens are in GGU 298969, 298970, 298974, and 298975.

Remarks. T. fissus is characterised by moderate to high cephalic convexity, a wide glabella, a median carina along the front half of the posteroglabella, usually poor to moderate development of genal pits and scrobiculae, and a lack of spines. Additional characters and the considerable morphological variability of *T. fissus* have been well described by Westergård (1946, pp. 58–59). New specimens from Greenland closely resemble those from the type area in Sweden and they show similar variability.

Occurrence. T. fissus is a common species that has been previously reported from Sweden, Norway, Denmark, England, Wales, Canada (eastern & western Newfoundland), United States (South Carolina), and Russia (Siberia). The new specimens are from the upper half of the Henson Gletscher Formation in Nyeboe Land where they are present in both the *Ptychagnostus gibbus* and *Ptychagnostus atavus* zones.

Tomagnostus perrugatus (Grönwall, 1902)

Fig. 31.2, 3, 1?

Agnostus fissus var. *perrugata* Grönwall, 1902, p. 50, pl. 1, fig. 1

not *Agnostus fissus* var. *perrugatus* Grönwall, Illing, 1916, p. 407, pl. 28, fig. 9 [? = *Tomagnostus fissus* (Linnarsson)]

Agnostus sulcatus Illing, 1916, pp. 411–412, pl. 30, figs 3–6

Goniagnostus sulcatus (Illing), Howell, 1935c, p. 14

Tomagnostus perrugatus (Grönwall), Kobayashi, 1939, pp. 149–150; Westergård, 1946, pp. 59–60, pl. 8, figs 1–10; Hutchinson, 1962, p. 77, pl. 7, figs 6–9; Savitsky *et al.*, 1972, p. 60, pl. 5, figs 7–10; Rushton, 1979, pp. 55–56, fig. 6C-E; Egorova, Pegel & Chernysheva *in* Egorova *et al.*, 1982, p. 59, pl. 17, figs 5, 6, pl. 54, figs 9, 12; Morris, 1988, p. 229

Tomagnostus sulcatus (Illing), Kobayashi, 1939, p. 149

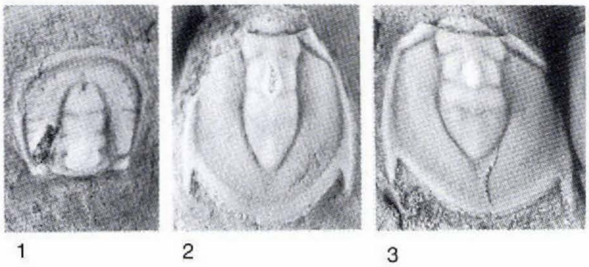


Fig. 31. *Tomagnostus perrugatus* (Grönwall). All specimens from GGU 319790. 1, questionably assigned, small holaspid cephalon, MGUH 21.466, × 10. 2, 3, pygidia, MGUH 21.467 and 21.468, both × 8.

Tomagnostus deformis Pokrovskaya, 1958, pp. 32–34, pl. 2, figs 5–9; Egorova, Pegel & Chernysheva *in* Egorova *et al.*, 1982 (in part), p. 60, pl. 5, fig. 5, ?pl. 12, fig. 13 (not pl. 8, fig. 9)

?*Tomagnostus perrugatus* West. [sic], Pokrovskaya, 1958, pl. 2, figs 10, 11

Agnostus sp. Šnajdr, 1958, p. 70, pl. 46, fig. 3

Tomagnostus renata Fatka *et al.*, 1981, pp. 368–369, pl. 2, figs 3–5

Tomagnostus cf. *perrugatus* (Grönwall), Fatka & Kordule, 1992, pl. 2, fig. 3

New material. Two pygidia are in GGU 319790. One cephalon in GGU 319789 and 2 cephala in GGU 319790 are questionably assigned to this species.

Emended diagnosis. Glabella narrow, tapering only slightly. Genae having many radial scrobiculae (abaxial) and pits (mostly adaxial), pair of arcuate grooves opposite front of glabella, and may have pair of short longitudinal grooves opposite M3. Transverse sulcus of posteroaxis having pair of tiny pits. Pygidial border flat, without or with collar, and with pair of marginal spines.

Remarks. Westergård (1946, pp. 59–60) has described well the morphological variability observed within populations of this species in Sweden. Two new pygidia from Greenland accord closely with his description. Cephala of *Tomagnostus* associated with the new pygidia are not well preserved and their identification to species is questionable.

Occurrence. Specimens representing *T. perrugatus* have been previously reported from Denmark, Sweden, England, Canada (eastern Newfoundland), Czechoslovakia, and Russia (Siberia). They have a composite observed stratigraphic range from the *Ptychagnostus gibbus* Zone to the *Ptychagnostus punctuosus* Zone. The new specimens from Greenland are from basal beds of the Kap Stanton Formation, and are from the *Ptychagnostus atavus* Zone.

Family unassigned

Genus *Megagnostus* n. gen.

Etymology. Greek *mega*, large, plus *Agnostus*; referring to the exceptionally large size of some specimens.

Type species. Agnostus glandiformis Angelin, 1851, pp. 5–6.

Diagnosis. Cephalon mostly effaced, retaining only vestiges of posterior border furrows; convexity low to moderate. Cephalic doublure narrow. Thorax with anterior segment sagittally longer than posterior segment; axial rings transversely wide, effaced. Pygidium characterised by unique doublure that curves inward and downward, forming ventrally projecting flange. Pygidium smaller than cephalon, with acrolobe effaced except for weak median node; convexity low. Border furrow of pygidium well developed or may become effaced posteriorly on large holaspides. Articulating half ring narrow sagittally, wide transversely; width averaging about half that of pygidium. Articulating furrow narrow, shallow. Spines absent.

Remarks. Agnostus glandiformis Angelin, 1851 has been assigned by various authors to at least five different genera (see synonymy below). Illustrations by Lindström (1901, pl. 1, fig. 7), Holm & Westergård (1930, pl. 1, fig. 4), and Westergård (1946, pl. 15, fig. 10a, b) show this species to have an unusual, prominent flange that projects ventrally from the pygidial doublure. The presence of a border demonstrates that the specimen illustrated by Holm & Westergård is a pygidium rather than a cephalon as stated in their figure caption. A similar flange is also present on a new agnostoid species from North Greenland (see Fig. 32.9a). This type of flange is considered to be a significant synapomorphous character, and is used with other characters in defining and differentiating the new genus *Megagnostus*. Included in this genus are *M. glandiformis* (Angelin), *M. diclidus* n. sp., and questionably *M. resecta* (Grönwall).

The prominent ventral flange on the pygidial doublure of *Megagnostus* is probably part of a coaptive device for interlocking the cephalon and pygidium during enrollment. To my knowledge, a similar device has not been reported in any other agnostoid genus.

A fine, asymmetric, submarginal groove also is present on the interior surface of the pygidial doublure of both *M. glandiformis* (see Fig. 33.4, 5, 12, 13) and *M. diclidus* (see Fig. 32.5, 7). It is commonly seen on internal moulds. Its position is remarkably similar to that of a submarginal suture on the cephalon of the Ordovician agnostoid *Arthrorhachis elspethi,* examples of which were described and illustrated by Hunt (1966) as *Trinodus elspethi.* The pygidial doublure of *Megagnostus,* however, shows no evidence of a functional suture.

In its style and advanced degree of effacement, *Megagnostus* closely resembles *Leiagnostus,* a widespread Lower Ordovician genus that has been recently revised by Ahlberg (1988). However, subtle morphological differences and a lack of likely connecting taxa in Upper Cambrian strata suggest that these genera are not closely related. The articulating half ring on the pygidium of *Megagnostus* is much wider transversely than in *Leiagnostus,* which may indicate important differences in the effaced axis of each genus. They also differ in such details as convexity of the pygidium and prominence of its median node, which are less in *Megagnostus.* Further review by Ahlberg (1992) has led to the suggestion that *Leiagnostus* may be a highly effaced derivative of *Lotagnostus* from Upper Cambrian strata, and of the family Agnostidae.

Affinities with other agnostoid genera are difficult to assess because of the high degree of both cephalic and pygidial effacement in *Megagnostus.* Widely spaced points of origin of posterior border furrows on the cephalon and a wide articulating half ring on the pygidium indicate an unusually wide, though mostly effaced axial lobe on both shields. All characters considered, *Megagnostus* most closely resembles *Phalacroma.* The phyletic significance of that resemblance is problematic, however, and the family assignment of *Megagnostus* is left open.

The taxonomic status of *Agnostus glandiformis* var. *resecta* Grönwall, 1902 is unclear. Westergård (1946, pp. 93–94, pl. 14, fig. 19) elevated the taxon to species rank and reassigned it to *Phalacroma* (see also Jago, 1976, p. 146, pl. 24, fig. 12). Additional specimens from Spain were attributed to the species by Sdzuy (1961, pp. 525–526, pl. 2, figs 10–13), but he reassigned it to *Leiagnostus* Jaekel, 1909. Pygidia that have been assigned to the species have a shallower border furrow and narrower border than do pygidia of *M. glandiformis* of comparable size, but are closely similar in other dorsal features. Until more information is available, especially regarding structure of the pygidial doublure, the species is questionably reassigned to *Megagnostus.*

Megagnostus is known from Sweden, Norway, Denmark, Greenland, Russia (Siberia), the United States (Vermont), Australia (Tasmania), and questionably from Canada (eastern Newfoundland), England, France, and Spain. Assigned specimens are from the *Lejopyge laevigata* Zone and some questionably assigned specimens (*M. ?resecta*) are from the subjacent *Ptychagnostus punctuosus* Zone and possibly older strata.

Megagnostus diclidus n. sp.

Fig. 32

Etymology. Greek *diklidos,* double folding; referring to the upturned lateral borders of the pygidium.

Holotype. Pygidium (Fig. 32.9a, b), MGUH 21.477 from GGU 301313.

Material. More than 50 disarticulated specimens are in GGU 301312, 301313, and 313115.

Diagnosis. Cephalon subquadrate, width and length usu-

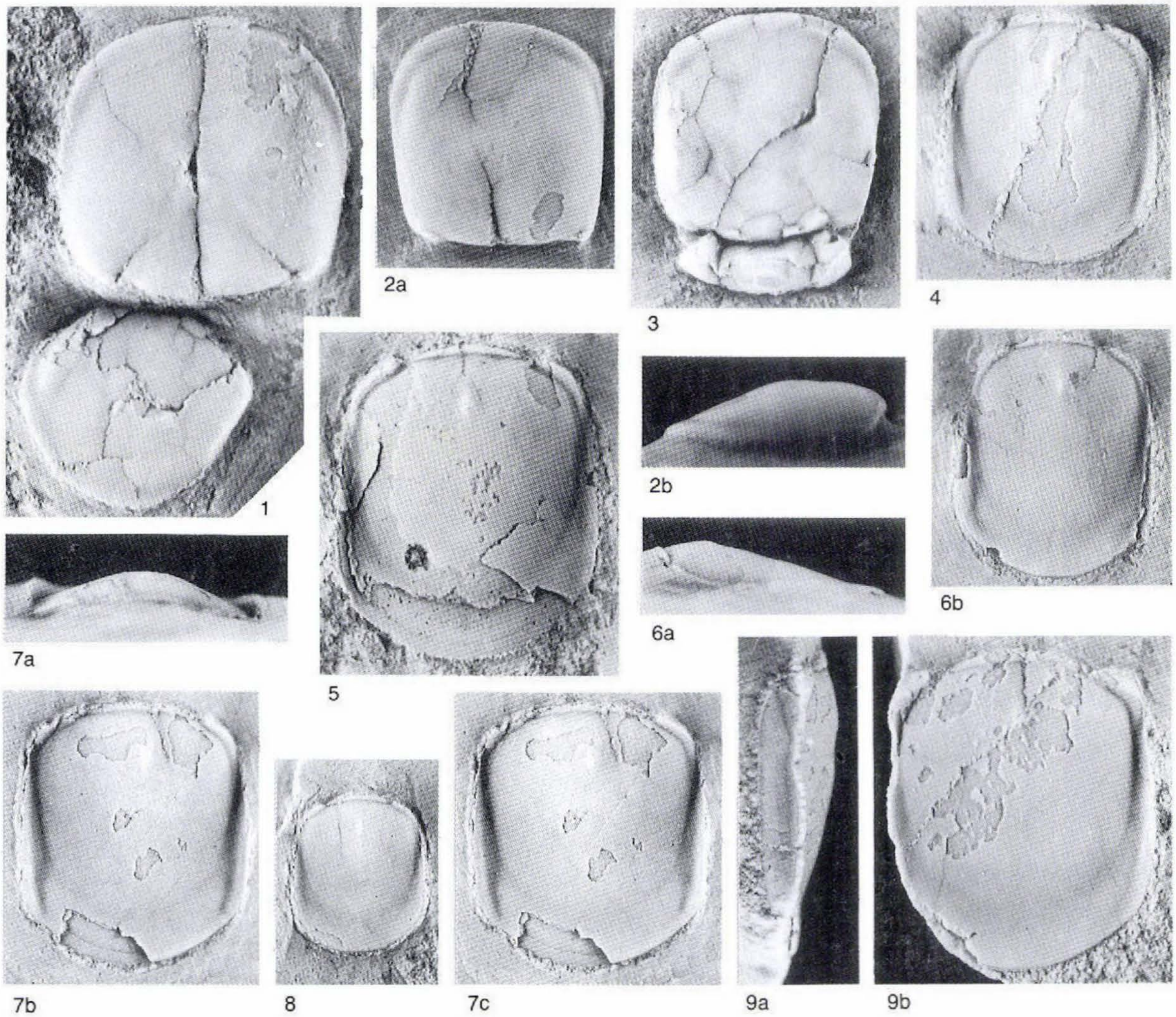


Fig. 32. *Megagnostus diclidus* n. gen. & n. sp. All specimens are from GGU 301313, unless otherwise stated. 1, two flattened cephala, MGUH 21.469, × 5. 2a, b, cephalon in dorsal and lateral views, MGUH 21.470 from GGU 313115, × 8. 3, cephalon and thorax, MGUH 21.471 from GGU 313115, × 7. 4, 5, pygidia, MGUH 21.472 and 21.473 from GGU 313115, × 8 and × 6. 6a, b, pygidium in lateral and dorsal views, MGUH 21.474, × 7. 7a-c, pygidium in frontal (a) and stereographic views (b, c), MGUH 21.475, × 7. 8, small holaspid pygidium, MGUH 21.476, × 8. 9a, b, holotype pygidium with exposed ventral flange (a), in lateral and dorsal views, MGUH 21.477, × 8.

ally about equal; convexity low. Thorax not known. Pygidium subrectangular, width averaging about 0.9 times that of length; convexity of acrolobe very low; median node elongate. Pygidial borders narrow and upturned laterally, diminishing in height posterolaterally, and undifferentiated posteriorly except in early holaspides.

Remarks. Middle and late holaspid pygidia of *M. diclidus* differ from those of *M. glandiformis* by having more upturned lateral borders and by lacking a differentiated posterior border furrow and border. To my knowledge, form of the late holaspid border of *M. diclidus* is unique among agnostoid trilobites. On early holaspid pygidia of comparable sise, the border and furrow development is similar in *M. diclidus* (Fig. 32.8) and *M. glandiformis* (see Fig. 33.9), suggesting close phyletic affinity. Because these two morphs are consistently associated in three collections from the Kap Stanton Formation, sexual dimorphism is a possible explanation for the observed differences. This seems unlikely, however, because the *glandiformis* morph has been illustrated from several localities around the world, whereas the *diclidus* morph is known from only North Greenland. The cephalon and pygidium of *M. diclidus* further differ from those of *M. glandiformis* by being less convex, and on average the cephalon is more quadrate and the pygidium is more rectangular. In sagittal profile, the pygidium of *M. diclidus* is angular with its apex coinciding with its median node (Fig. 32.6a), whereas the pygidium of *M. glandiformis* is broadly rounded with little perceptible change in slope at its median node (see Fig. 33.3b, 12b).

Maximum observed size also differs significantly between *M. diclidus* and *M. glandiformis.* The largest observed cephalon of *M. diclidus* is 7.6 mm long. The largest cephalon of *M. glandiformis* in GGU collections is 14.0 mm long, whereas Westergård (1946, p. 96) noted that the largest cephalon in Swedish collections is 16.0 mm long.

Occurrence. All specimens of *M. diclidus* are from basal beds of the Kap Stanton Formation in Peary Land, and are from the lower *Lejopyge laevigata* Zone.

Megagnostus glandiformis (Angelin, 1851)

Fig. 33

Agnostus glandiformis Angelin, 1851, pp. 5–6, pl. 6, fig. 1; Brøgger, 1878, p. 74, pl. 6, fig. 7; Tullberg, 1880, pp. 29–30, pl. 2, fig. 20a, b; Lindström, 1901, p. 37, pl. 1, fig. 7; Grönwall, 1902 (in part), pp. 63–64 (not pl. 1, fig. 6); Westergård *in* Holm & Westergård, 1930, pp. 10–11, pl. 1, figs 2–5, pl. 4, figs 1–3

Leiagnostus glandiformis (Angelin), Jaekel, 1909, p. 401; Sdzuy, 1961, p. 526

?*Agnostus glandiformis* Angelin, Illing, 1916, p. 414, pl. 31, fig. 2 [specimen refigured as *Grandagnostus* sp. by Rushton, 1979, fig. 4C]

Grandagnostus vermontensis Howell, 1935a (in part), p. 221, pl. 22, figs 9?, 10?, 11 (not 8); Howell, 1937 (in part), pp. 1166–1167, pl. 3, figs 6?, 8?, 9 (not 5); Shaw, 1966, p. 848, pl. 97, fig. 10?

Grandagnostus glandiformis (Angelin), Howell, 1935a, p. 221; Lermontova, 1940, p. 131, pl. 36, figs 7, 7a-j; Poulsen, 1969, pp. 7–9, figs 7A-C; Jago, 1976, pp. 144–146 [compared with other species in discussion of *Valenagnostus*], pl. 24, figs 1–5

Phalacroma glandiformis (Angelin), Kobayashi, 1939, pp. 136–139

?*Grandagnostus longifrons* Lermontova, 1940, p. 131, pl. 36, figs 8, 8a-d

Phalacroma glandiforme (Angelin), Westergård, 1946, pp. 95–97, pl. 15, figs 3–17, pl. 16, figs 1, 2; Pokrovskaya, 1958, pp. 53–56, pl. 4, figs 1–6; Pokrovskaya *in* Chernysheva, 1960, pl. 1, figs 26, 27; Khajrullina, 1970, p. 17, pl. 1, fig. 14; Khajrullina, 1973, pp. 48–49, pl. 3, fig. 15; Egorova, Pegel & Chernysheva *in* Egorova *et al.*, 1982, p. 74, pl. 22, ?fig. 6, pl. 23, ?fig. 5, pl. 49, fig. 1, pl. 55, figs 12, 13, pl. 59, fig. 5, pl. 62, fig. 9

?*Phalacroma maja* Pokrovskaya, 1958, pp. 50–51, pl. 4, figs 9–12; Egorova, Pegel & Chernysheva *in* Egorova *et al.*, 1982, pp. 74–75, pl. 19, fig. 2, pl. 20, fig. 8, pl. 23, fig. 4, pl. 25, fig. 3, pl. 40, fig. 1, 2, pl. 47, fig. 2, 3, pl. 59, fig. 4, pl. 62, fig. 4

?*Phalacroma longifrons* (Lermontova), Pokrovskaya, 1958, pp. 52–53, pl. 4, figs 13–15; Egorova, Pegel & Chernysheva *in* Egorova *et al.*, 1982, p. 75, pl. 15, fig. 4, pl. 30, fig. 1

Phalagnostus glandiformis (Angelin), Rosova, 1964, pp. 17–18, pl. 2, figs 14–21, pl. 3, fig. 3; Poulsen, 1966, p. 122; Repina *et al.*, 1975, pp. 118–119, ?pl. 11, figs 20, 21

?*Phalagnostus cuneatus* Rosova, 1964, pp. 18–19, pl. 2, fig. 22, pl. 3, figs 10–12

?*Lejopyge laevigata* (Dalman), Poulsen & Anderson, 1975, pp. 2075–2076, pl. 2, figs 1–9 [see remarks on *Peratagnostus cicer*]

Grandagnostus sp. Jago, 1976, pp. 141–142, pl. 22, figs 1–5

?*Grandagnostus major* Courtessole *et al.*, 1988, p. 36, pl. 1, figs 6–11, ?pl. 8, fig. 7

Lectotype. Cephalon (State Museum of Natural History, Stockholm) selected and illustrated by Westergård (1946, p. 95, pl. 15, fig. 6).

New material. More than 50 disarticulated specimens are in GGU 301312, 301313, and 313115.

Emended diagnosis. Cephalon subcircular to subpentagonal with broadly pointed anterior margin, width ranging from about 0.9 to 1.0 times that of length; convexity moderate to high. Pygidium subcircular to subpentagonal, width ranging from about 0.9 to 1.0 times that of length; convexity low. Border furrow of pygidium broad and shallow; border widens posteromedially on early holaspides, becoming narrow and more uniform on later holaspides. Dorsal exoskeleton finely punctate.

Remarks. From populations of *M. glandiformis* in Sweden, Westergård (1946, p. 96) noted that the ratio of length to width for both cephala and pygidia is greatly variable, even for specimens retaining original convexity. In dorsal view, the outlines of both shields also vary from subcircular (common in early holaspides) to subpentagonal (common in later holaspides). Many new specimens from Greenland possess the diagnostic characters of *M. glandiformis* and show similar ranges of morphological variation.

M. glandiformis is characterised by extreme effacement of dorsal features, including basal lobes, glabellar median node, and all but posterior vestiges of the cephalic border furrow. Jago (1976, p. 146) stated that some specimens possess vestigial basal lobes. On specimens I have observed, however, the basal lobes are expressed only as weak swellings if preservation is good. Some large cephala have a submarginal, ventral ridge formed by angular folding of the doublure. Where exposed by exfoliation, that ridge superficially resembles a border furrow (Fig. 33.7), and could be mistaken for such. Well-preserved topotype specimens from Sweden, seemingly retaining original convexity, are illustrated here (Fig.

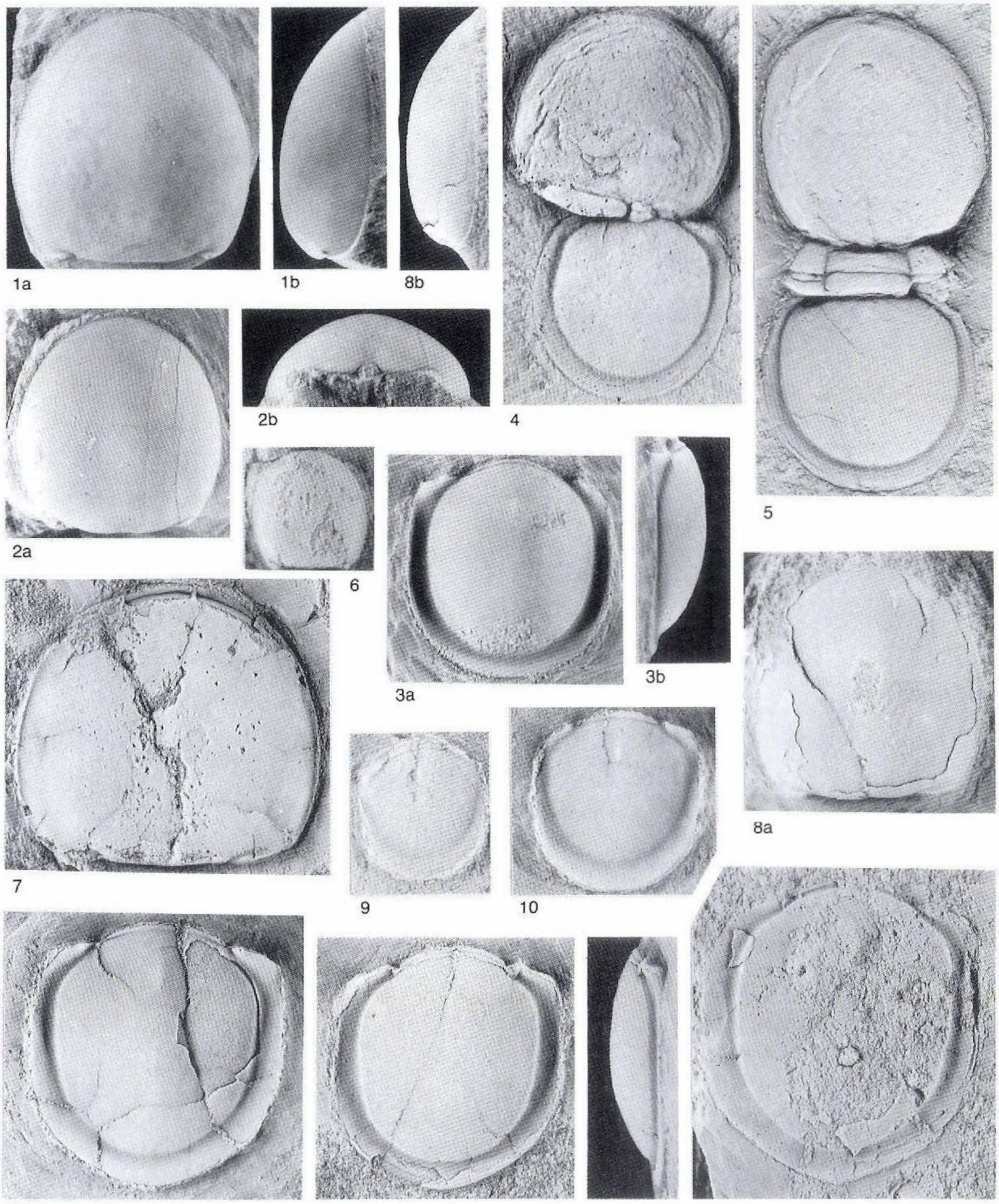


Fig. 33. *Megagnostus glandiformis* (Angelin) n. gen. 1–3, comparative topotype specimens from Andrarum Limestone, Sweden; 1a, b, cephalon in dorsal and lateral views, U.S. National Museum of Natural History (USNM) no. 465529, × 3; 2a, b, cephalon in dorsal and rear views, USNM 465530, × 4; 3a, b, pygidium in dorsal and lateral views, USNM 465531, × 3. 4, 5, comparative specimens collected by William V. Murray from the Skeels Corners Formation, Vermont, showing wrinkles on cephala from compression in shale, USNM 465532 and 465533, × 3 and × 6. 6, small holaspid cephalon, MGUH 21.478 from GGU 313115, × 8. 7, large holaspid cephalon, partially flattened, MGUH 21.479 from GGU 301313, × 3. 8a, b, cephalon in dorsal and lateral views, MGUH 21.480 from GGU 301313, × 3. 9, 10, small holaspid pygidia from GGU 301313, MGUH 21.481 and 21.482, both × 8. 11, pygidium, MGUH 21.483 from GGU 313115, × 4. 12a, b, pygidium in dorsal and lateral views, MGUH 21.484 from GGU 313115, × 3. 13, large holaspid pygidium, MGUH 21.485 from GGU 301313, × 3.

33.1–3) for comparison with new specimens from Greenland, which have been variably compressed in fine-grained matrix.

The holotype of *Grandagnostus vermontensis* Howell, 1935a, which is the type species of *Grandagnostus* Howell, 1935a, is a poorly preserved, incomplete, smooth, probable cephalon that was recently discussed and reillustrated (Robison, 1988, p. 53, fig. 12.7). In the absence of definitive characters, I proposed that the name *Grandagnostus* be restricted to the holotype of *G. vermontensis.* My support for that proposal has not changed, and I here consider *Grandagnostus* to be an unrecognisable genus. Two specimens of *M. glandiformis* from a new locality in Vermont are illustrated here (Fig. 33.4, 5) for comparison with specimens from Sweden and Greenland. I have also examined other specimens that were originally illustrated as *G. vermontensis,* which are here reassigned to *M. glandiformis* (see synonymy for references).

In a subsequent diagnosis of *Grandagnostus* Shergold *et al.* (1990, p. 55) stated that the cephalic border is narrow or absent and the glabellar node is advanced. The holotype of the type species, however, shows no evidence of either a cephalic border or a glabellar node, although the configuration of adjacent matrix does superficially resemble an incomplete border.

Based on observed morphological variation in populations of *M. glandiformis* in Sweden and Greenland, I suggest that *Grandagnostus longifrons* Lermontova, 1940, *Phalacroma maja* Pokrovskaya, 1958, and *Phalagnostus cuneatus* Rosova, 1964 may be based on geographic variants of *M. glandiformis* in which length of the cephalon and angularity of its anterior margin are slightly accentuated. Without access to type collections, however, I reassign the specimens to *M. glandiformis* with question. At least two of the specimens illustrated as *Phalacroma maja* by Egorova, Pegel & Chernysheva (*in* Egorova *et al.*, 1982, pl. 47, figs 2, 3) appear to represent *M. glandiformis.*

M. glandiformis has the distinction of including the largest known specimens of the order Agnostida, which in size are substantially larger than average for the order. Westergård (1946, p. 96) noted that the species is the largest agnostoid found in Scandinavia, and he reported the largest cephalon to be 16.0 mm long and 15.0 mm wide. A flattened cephalon in GGU 301313 (Fig. 33.7) is 14.2 mm long. The largest specimen from Greenland is a poorly preserved, incomplete pygidium in GGU 313115. It is 16.5 mm wide, but its length is indeterminate because of breakage. Although cracks indicate that its width may have been increased slightly by compression, it is relevant that the pygidium is smaller than the associated cephalon in this species (Fig. 33.4, 5; see also Westergård, 1946, pl. 15, fig. 13a-d). Therefore, GGU 313115 may contain the largest observed agnostoid trilobite.

Occurrence. M. glandiformis is a widespread species, having been previously reported from Sweden, Norway, Denmark, Russia (Siberia), the United States (Vermont), Greenland (Nyeboe Land), Australia (Tasmania), and questionably from Canada (eastern Newfoundland), England, and France. The new specimens from Greenland are all from basal beds of the Kap Stanton Formation in Peary Land, and are from the lower *Lejopyge laevigata* Zone. Most reported occurrences of the species are from the *L. laevigata* Zone, however, it questionably ranges as low as the *Ptychagnostus atavus* Zone.

Genus *Peratagnostus* Öpik, 1967

Peratagnostus Öpik, 1967, pp. 86–87; Palmer, 1968, p. B26; Shergold, 1982, pp. 21–22; Shergold *et al.*, 1990, pp. 43–44

Type species. Peratagnostus nobilis Öpik, 1967, pp. 87–90.

Emended diagnosis. Cephalon mostly effaced, but retaining posterior border furrows, vestiges of basal furrows, and weak median node at about midlength; convexity moderate to high. Posterior vestige of glabella rounded. Thorax having transversely wide, effaced axial rings; pleural furrows weak. Pygidial ontogeny characterised by unusual, abrupt early holaspid metamorphosis during which border furrow first developed; subsequently, axial lobe increased in relative length and width as axial furrow became posteriorly effaced or entirely effaced; ring furrows undeveloped throughout ontogeny. Late holaspid pygidium highly convex; median node poorly defined, elongate. Articulating half ring of late holaspides variable in transverse width, being greater than half that of pygidium during early phylogeny and becoming less than half that of pygidium during later phylogeny. Spines absent.

Remarks. The concept of *Peratagnostus* has commonly been applied to species from only Upper Cambrian strata (e.g., Shergold *et al.* 1990, pp. 43–44). Based in part on character transformations during both ontogeny and inferred phylogeny, that concept is expanded here to include reassignment of *Agnostus cicer* Tullberg, 1880 and other species in Middle Cambrian strata.

The cephalon of *Peratagnostus* is characterised by advanced effacement of furrows, which may make the identification of disarticulated cephala difficult in collections containing other effaced genera. On some holaspid cephala the glabella may be indicated by a vestigial posterior swelling, and in some meraspid cephala the posteroglabella may be weakly outlined. In all but possibly one species, *P. hillardensis* Palmer, 1968, even the border furrow is effaced except for vestiges along the posterior cephalic margin. In discussing *Grandagnostus falanensis* (Westergård), which is herein reassigned to *Peratagnostus*, Rushton (1978, p. 257) noted that some internal moulds from England have lateral and frontal grooves that resemble a cephalic border furrow, but they represent the inner edge of the cephalic doublure. The single illustrated cephalon of *P. hillardensis* (Palmer, 1968, pl. 10, fig. 17) may also be an internal mould, and therefore warrants further investigation of its reputed marginal groove.

New specimens of *P. cicer* from North Greenland include distinctive juvenile pygidia (see Fig. 34.1, 2) that closely resemble some pygidia previously assigned by Shergold (1982, pl. 6, figs 4–7) to *P. nobilis* Öpik, the type species of *Peratagnostus*. A significant character of these pygidia is a prominent, somewhat semicircular furrow on the dorsal surface. This, in reference to positions of the anterior border furrows, is identified as an axial furrow. Therefore, the largest of these pygidia are characterised by a well-defined, short, tumid axis with no ring furrows, and lateral and posterior parts of the border furrow are not evident.

In his study of *P. nobilis,* Shergold (1982, pp. 22–23) noted that pygidia with lengths less than 1.10 mm "are decidedly different from those with lengths greater than 1.50 mm, and are considered to represent meraspid growth stages." He also noted that "no specimens with lengths between 1.10–1.50 have been observed," and he concluded that if the smaller pygidia are to be regarded as *P. nobilis,* "then a substantial pygidial metamorphosis accompanies the change from meraspid to holaspid morphogenetic stages." A similar metamorphosis and a similar size gap between growth phases is indicated by specimens of *P. cicer* (see Fig. 34). Pygidia in the smaller growth phase range up to 1.1 mm in length and observed pygidia in the larger phase commence at 1.4 mm in length. Combined with general holaspid characters, I consider the distinctive juvenile morphology, evidence of dual growth phases, and the remarkably similar styles of metamorphosis to indicate a close taxonomic relationship between these two species, and to support their inclusion in the same genus.

The smallest pygidium of *P. cicer* in collection GGU 313115 from Greenland (see Fig. 34.1) has one axial ring, indicating that it represents degree 1 of the meraspid period (Robison, 1964, pp. 516–518). An apparent lack of axial rings on any of Shergold's (1982, pl. 6, figs 4–7) specimens of *P. nobilis* suggests that they are all holaspides. Therefore, the metamorphosis in both *P. nobilis* and *P. cicer* seems to have occurred during the early holaspid period. In some modern marine arthropods showing dual growth phases, the gap between them corresponds to onset of sexual maturity (Hartnoll, 1982). Although the same may be true for *Peratagnostus*, the rather abrupt change in form at very small body size may suggest some other cause. Changes in trophic resources, temperature, or mode of life are suggested as possible alternatives.

Although proportions of the pygidial axis are very similar in juveniles of *P. cicer* and *P. nobilis* (compare Fig. 34.1, 2 with Shergold, 1982, pl. 6, figs 4–7), they are quite different in large adults (compare Fig. 34.7, 8 with Öpik, 1967, text-fig. 18 and Palmer, 1968, pl. 10, fig. 24). *P. cicer* also retains vestiges of the axial furrow. Axial proportions of intermediate holaspid pygidia of *P. cicer* (see Fig. 34.3, 4) accord with a possibility that the late holaspid axis of *P. nobilis* is paedomorphic with respect to that of *P. cicer*, its inferred ancestor. Thus, I attach trivial rather than generic significance to the late holaspid difference in axial proportions.

Juvenile specimens of *Phalagnostus nudus* (Beyrich, 1845), the type species of *Phalagnostus* Howell, 1955, are closely similar to those of *Peratagnostus*. In *Phalagnostus,* however, the distinctive juvenile characters are retained essentially unaltered into the late holaspid period (compare Šnajdr, 1958, pl. 5, figs 1–24). These persistent characters include a prominent semicircular axis and absence of cephalic and pygidial border furrows except for proximal vestiges along margins adjacent to the thorax. Based on shared characters, I suggest that *Peratagnostus* and *Phalagnostus* are closely related, and that *Phalagnostus* probably arose from *Peratagnostus* by paedomorphic retention of juvenile characters into the late holaspid period. *Phalagnostus* can be differentiated from *Peratagnostus* by the absence of a metamorphosis during ontogeny and by the related absence of two distinct growth phases. Late holaspid characters, or course, are quite different. As in modern marine arthropods (Williamson, 1982, p. 92), ontogeny within these genera seems to be "a reminder that adult and larval evolution can sometimes proceed independently."

Other species of *Peratagnostus*, as emended, are also present in Middle Cambrian strata. One of these is *Ciceragnostus? falanensis* Westergård, 1947. Rushton (1978, pp. 256–258) reassigned this species to *Grandagnostus*, and he suppressed *Phalacroma bairdi* Hutchinson (1962, pp. 90–91) as a junior synonym. Additional specimens were subsequently discussed and illustrated by Rushton (1983, p. 117, pl. 15, figs 2–5, 8, 9) from younger strata. As mentioned above in remarks on *Megagnostus glandiformis, Grandagnostus* is considered to be an unrecognisable genus. In degree of effacement, specimens of *falanensis* resemble those of both *Megagnostus* and *Per-*

atagnostus. In convexity and mammiform transverse profile of its pygidium, however, they resemble specimens of only *Peratagnostus*. Therefore, *falanensis* is here reassigned to *Peratagnostus*, and I concur with Rushton that *Phalacroma bairdi* Hutchinson is a junior synonym. *P. falanensis* seems to be a direct descendent of *P. cicer*, from which it mainly differs by its axial furrow being more effaced on the late holaspid pygidium. *P. cicer* has an observed stratigraphic range in the Middle Cambrian from the *Ptychagnostus atavus* Zone into the *Lejopyge laevigata* Zone, and *P. falanensis* has a reported stratigraphic range from the uppermost Middle Cambrian (uppermost *Lejopyge laevigata* Zone) to the middle Upper Cambrian (upper *Olenus* Zone).

In addition to *P. cicer* (see synonymy below), other species of *Peratagnostus* have been reported from multiple localities in the upper Middle Cambrian of China. *P. sinicus* was named by Hsiang *in* Egorova *et al.* (1963) and has been further documented by Lu *et al.* (1965, p. 39, pl. 3, figs 23–25), Xiang *et al.* (1981, p. 118, pl. 7, figs 16, 17), and Xiang & Zhang (1985, p. 70, pl. 14, figs 1–4). '*Peratagnostus exilis* n. sp.' has been recorded on a biostratigraphic chart of taxa identified by Dong (1990, fig. 1) from a late Middle Cambrian section in western Hunan, China. Although the generic assignment of Dong's specimens may be correct, the new species name seems to be a *nomen nudum.* In an unpublished thesis by Song (1989, p. 46, pl. 3, figs 3–6), an undetermined species of *Peratagnostus* has been described and illustrated from the *Lejopyge laevigata* Zone of the same section in western Hunan.

One or more undetermined species of *Peratagnostus* may be represented by several distinctive juvenile specimens from the *Lejopyge laevigata* Zone. These include one pygidium from Sweden that Westergård (1946, p. 97, pl. 16, fig. 3) identified as *Phalacroma* sp., several pygidia from the Taconic sequence of New York that Rasetti (1967, pp. 38–39, pl. 10, figs 22–26) assigned as 'Agnostida, pygidium no. 1,' and two pygidia from Tasmania that Jago (1976, p. 168, pl. 26, fig. 15) assigned as 'Agnostid, gen. et sp. indet. no. 1.'

Several agnostoid species from Upper Cambrian strata have previously been assigned or reassigned to *Peratagnostus*. These have been reviewed in detail by Palmer (1968, p. B26) and Shergold (1982, pp. 21–22).

In posterior view, a mammiform profile may be characteristic of most or all late holaspid pygidia of *Peratagnostus*, as emended. Examples have been illustrated by Öpik (1967, pl. 52, fig. llb), Rushton (1978, pl. 24, figs 9, 11), and Song (1989, pl. 3, fig. 8b). Others are shown here (see Fig. 34.6c, 8a).

Peratagnostus, as emended, is geographically widespread in open-marine environments, and it has an observed stratigraphic range from the *Ptychagnostus atavus* Zone in the middle Middle Cambrian to the middle Upper Cambrian (for summary of Upper Cambrian occurrences, see Shergold *et al.*, 1990, p. 44).

Peratagnostus cicer (Tullberg, 1880)

Fig. 34

Agnostus cicer Tullberg, 1880, pp. 26–27, pl. 2, fig. 16a, b; Linnarsson, 1883, p. 32; Grönwall, 1902, p. 59

Agnostus cicer var. *forfex* Grönwall, 1902, pp. 59–60, pl. 1, fig. 5

Miagnostus cicer (Tullberg), Jaekel, 1909, p. 401

Ciceragnostus cicer (Tullberg), Westergård, 1946, pp. 90–91, pl. 14, figs 4–9; Pokrovskaya *in* Chernysheva, 1960, pl. 1, fig. 29; Hutchinson, 1962, p. 89, pl. 10, figs 15, 16, pl. 11, figs 1, 2; Öpik, 1967, p. 76; Yang, 1978, pp. 19–20, pl. 1, figs 8, 9; Yang, 1982, pl. 2, fig. 4; Egorova, Pegel & Chernysheva *in* Egorova *et al.*, 1982 (in part), p. 73, ?pl. 18, fig. 1, pl. 23, fig. 3; pl. 54, fig. 8; ?pl. 61, figs 3, 4 (not pl. 19, fig. 4)

Ciceragnostus cf. *cicer* (Tullberg), Westergård, 1946, pl. 16, fig. 6a, b

?'*Agnostus*' sp. No. 3 Westergård, 1946, p. 97, pl. 16, fig. 12a, b

New material. One complete specimen is in GGU 301313 (Fig. 34.7) and about 20 pygidia are in GGU 301312, 301313, and 313115. Several small cephala of this species are probably present in the same collections, but confident differentiation of these from associated small cephala of *Megagnostus glandiformis* and *Toragnostus bituberculatus* has not been possible, partly because of advanced effacement of the cephalon in all three species and partly because of inadequate preservation.

Emended diagnosis. Peratagnostus with cephalon mostly effaced and highly convex.

Pygidium variably effaced, with axial furrow progressively disappearing from posterior in early and middle holaspides. Late holaspid acrolobe tumid, mammiform in transverse profile. Axis commonly constricted at position of M2 in middle and late holaspides; separated from posterior border furrow in early holaspides, lengthening to reach furrow in middle holaspides; width less than half that of pygidium in early holaspides, increasing to more than half in late holaspides. Median axial node weak to well defined, usually elongate. Border furrow narrow in early holaspides, broadening and shallowing in later holaspides. Border convex in early holaspides, becoming flat or downsloping in later holaspides, especially toward posterior.

Remarks. Advanced effacement of some features, especially those of the cephalon, has hindered phylogenetic analysis of *Agnostus cicer* Tullberg, 1880, and its generic

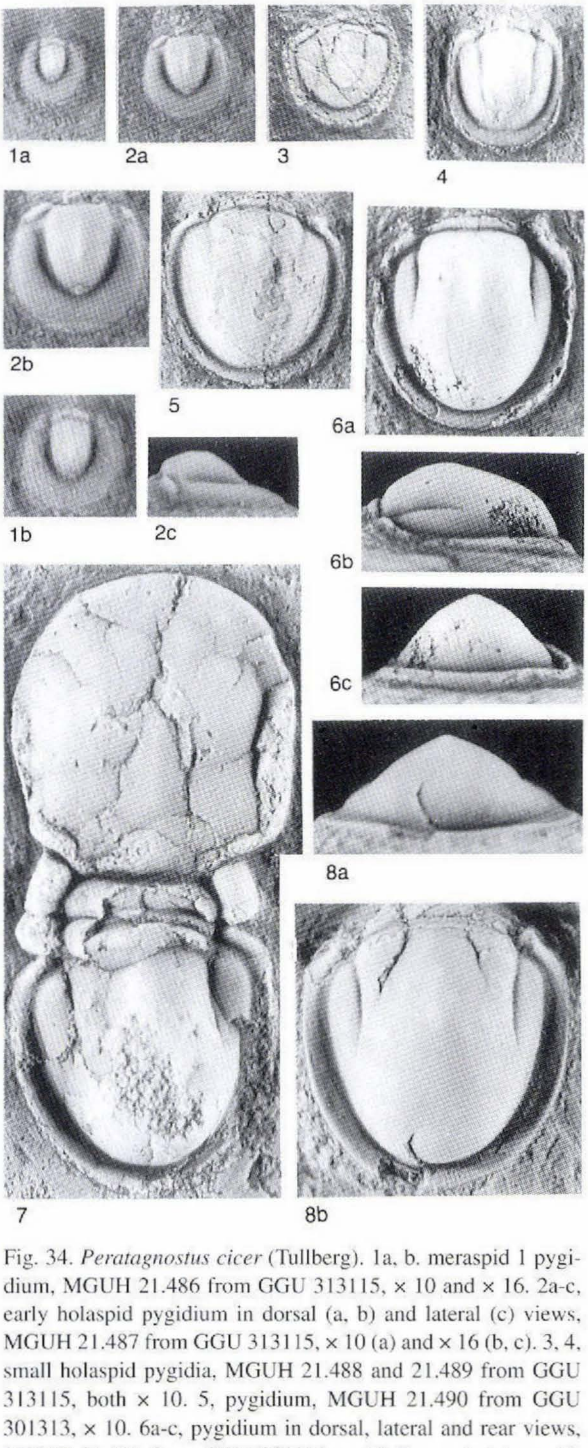


Fig. 34. *Peratagnostus cicer* (Tullberg). 1a, b. meraspid 1 pygidium, MGUH 21.486 from GGU 313115, × 10 and × 16. 2a-c, early holaspid pygidium in dorsal (a, b) and lateral (c) views, MGUH 21.487 from GGU 313115, × 10 (a) and × 16 (b, c). 3, 4, small holaspid pygidia, MGUH 21.488 and 21.489 from GGU 313115, both × 10. 5, pygidium, MGUH 21.490 from GGU 301313, × 10. 6a-c, pygidium in dorsal, lateral and rear views, MGUH 21.491 from GGU 301313, × 10. 7, exoskeleton with cracked and flattened cephalon, MGUH 21.492 from GGU 301313, × 8. 8a, b, large pygidium in rear and dorsal views, with inner margin of doublure exposed where rear border is broken, MGUH 21.493 from GGU 301313, × 8.

assignment has been problematic. Although *A. cicer* was reassigned to *Ciceragnostus* by Westergård (1946, pp. 90–91), it probably is not closely related to *Agnostus barlowi* Belt, 1868, the type species of *Ciceragnostus* (compare Morris & Fortey, 1985, pl. 1, fig. 1), a species of Early Ordovician (Tremadocian) age. According to Shergold *et al.* (1990, p. 55), *Ciceragnostus* is characterised by a narrow cephalic border and probably is an effaced pseudagnostid. In comparison, *A. cicer* lacks all but posterior vestiges of a cephalic border and it shows no evidence of a pseudagnostid deuterolobe.

Reasons for reassignment of *A. cicer* to *Peratagnostus* are given above in remarks on the genus. This reassignment is based on both juvenile and adult characters, and especially those of the pygidium.

P. cicer, as emended, is an agnostoid species showing greater than usual ontogenetic variability in some features of the pygidium. Also, similar variability is present in populations from both Sweden and North Greenland. Rates of ontogenetic increase in length to width ratio were greater for the axis than for the entire pygidium (compare pygidia in Fig. 34). Westergård (1946, p. 90) noted that the axis of small pygidia (less than 1.5 mm in length) is usually outlined throughout, this being a juvenile feature persisting in rare adults, and a feature used by Grönwall (1902) to distinguish the variety *forfex*. Minor differences in length to width ratios of the cephalon and pygidium may result from taphonomic deformation and should be used with care in taxonomy of such species as *P. cicer*. If compression is extreme, posterolateral edges may collapse under the cephalon (e.g., Fig. 34.7), and may further affect the cephalic length to width ratio.

Occurrence. P. cicer, as emended, is known from Denmark, Sweden, the United States (Vermont), China (Hunan, Guizhou), Russia (Siberia), and Greenland. The new specimens are from basal beds of the Kap Stanton Formation in Peary Land, and are from the lower *Lejopyge laevigata* Zone. The occurrence in Vermont is a new report based on a single, articulated exoskeleton from the Skeels Corners Formation. The Vermont specimen was collected by W. V. Murray, and its description is being prepared for inclusion in a separate publication. The observed stratigraphic range of *P. cicer* is from the *Ptychagnostus atavus* Zone to the *Lejopyge laevigata* Zone in the Middle Cambrian.

Genus *Phalagnostus* Howell, 1955

Type species. Battus nudus Beyrich, 1845, p. 46.

Remarks. Based on the position of anterior border furrows, Rasetti (1967, pp. 38–39) concluded that the prominent subcircular furrow on the pygidium of *Phalagnostus* is an axial furrow rather than a border furrow. That interpretation has been supported by Poulsen (1969, p. 9), Jago (1976, p. 146), and Rushton (1978, pp. 255–256). If correct, *Phalagnostus* is an exceptional agnostoid in its lack of both lateral and posterior borders on the late holaspid pygidium.

Phalagnostus ovalis (Illing, 1916)

Fig. 35

Agnostus nudus (Beyrich) var. *ovalis* Illing, 1916, p. 415, pl. 31, figs 9, 10

Phalacromina ovalis (Illing), Kobayashi, 1962, p. 29

Phalagnostus ovalis (Illing), Rushton, 1979, p. 60, fig. 9D; Morris, 1988, pp. 174–175

not *Phalagnostus ovalis* Yang, 1982, pp. 302–303, pl. 2, fig. 1 [regarded as secondary homonym, now *Pseudophalacroma ovalis* (Yang, 1982); 1985 International Code of Zoological Nomenclature, Article 57(c)]

New material. More than 20 specimens are in GGU 298970, 298975, 319789, and 319790.

Emended diagnosis. Cephalon ovoid, moderately convex posteriorly. Axial furrow weakly defined posteriorly, disappearing anteriorly from near basal lobes. Border furrow weak posteriorly, absent laterally and anteriorly.

Pygidium ovoid, having low relief, except for axis. Axial furrow wide, moderately deep. Axis subcircular to subquadrate, lacking ring furrows; median node weak, carinate. Pleural fields unusually flat, slightly downsloping; confluent posteriorly; width more than doubling from anterior to posterior. Border furrow weak anteriorly, absent laterally and posteriorly.

Remarks. P. ovalis was previously known from only a single enrolled specimen from England, which Rushton (1979) designated as the lectotype. New specimens from Greenland are closely similar, but the pygidial axis on larger holaspides is slightly more elongate. The axis appears to have become more elongate during ontogeny, so I do not regard that difference to be of taxonomic importance.

This species is the type of *Phalacromina* Kobayashi (1962, p. 29), which Rushton (1978, p. 256) suppressed as a subjective synonym of *Phalagnostus*. I concur with that action.

Occurrence. P. ovalis has been previously reported from horizon C2 in the Abbey Shales of the English Midlands. In North Greenland it is in collections from the upper Henson Gletscher Formation and from basal beds of the Kap Stanton Formation. Observed specimens from both England and Greenland are from the *Ptychagnostus atavus* Zone.

Genus *Schismagnostus* n. gen.

Etymology. Greek *schisma,* cleft or split, plus *Agnostus*; referring to the extraordinarily long frontal sulcus of the juvenile glabella.

Type species. Schismagnostus plicatus n. sp.

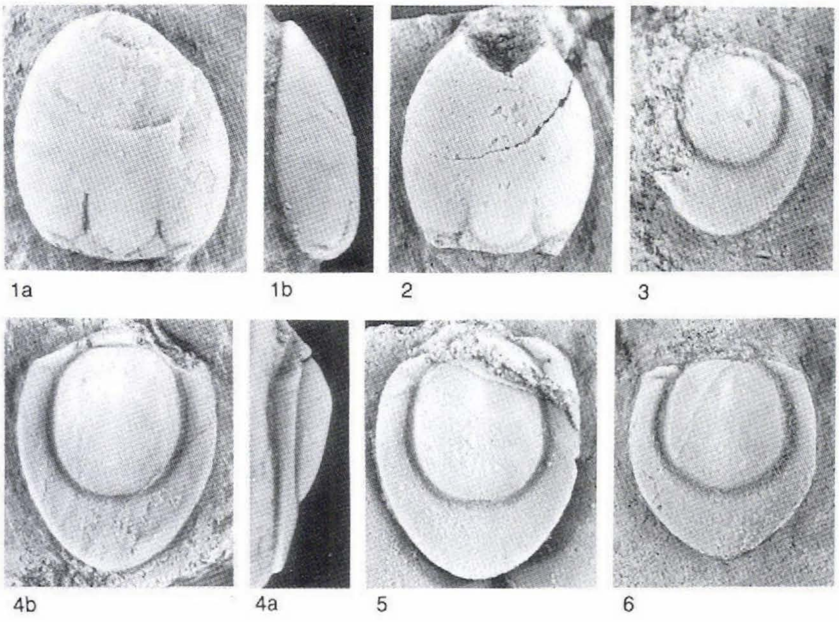


Fig. 35. *Phalagnostus ovalis* (Illing). All specimens from GGU 298970. 1, partly exfoliated cephalon in dorsal and lateral views, MGUH 21.494, × 8. 2, damaged cephalon, MGUH 21.495, × 8. 3, 6, smaller pygidia, MGUH 21.496 and 21.497, both × 10. 4, large pygidium in dorsal and lateral views, MGUH 21.498, × 8. 5, damaged pygidium, MGUH 21.499, × 8.

Diagnosis. Cephalon subquadrate. Glabella subcylindrical, bipartite with F3 bowed rearward; F1 and F2 prominent. Basal lobes simple to slightly elongate. Genae having abundant scrobicular grooves and pits; separated by preglabellar median depression, which may contain finer scrobiculae. Border narrow to moderately wide. Glabella of early instars having extraordinarily long frontal sulcus, extending rearward to about level of F2.

Thorax not known.

Pygidium subquadrate with pair of posterolateral border spines. Axis variable in length, subcylindrical with slight constriction at M2 and pointed posterior end; F1 weak, slightly bowed forward; F2 weak, straight to slightly bowed forward; median tubercle ovate, moderately large, confined to M2, and not interrupting F2. Posteroaxis slightly ogival, having shallow transverse sulcus with median node. Postaxial median furrow present and deep if axis is reduced in length. Border furrow moderately wide to wide.

Remarks. Schismagnostus is characterised by greater morphological change in the cephalon than is usual in other agnostoid genera during holaspid ontogeny. Beginning at least with early holaspid specimens, the cephalon already has well-developed genal scrobiculae, the anteroglabella is unusually small, and a deep frontal sulcus penetrates the anteroglabella and continues well back into the posteroglabella. To my knowledge, this is the only agnostoid with a frontal sulcus extending into the posteroglabella. On later holaspid specimens the frontal sulcus is entirely effaced, which seems to have occurred abruptly, perhaps between instars. At the same time, the anteroglabella was substantially enlarged. In the preceding diagnosis, however, late holaspid characters are emphasised because descriptions of agnostoid genera have been generally based on characters of that ontogenetic stage.

Late holaspid specimens of *Schismagnostus* resemble those of some species of *Tomagnostus* in such characters as pattern of genal scrobiculae and presence of a transverse sulcus on the posteroaxis. Representative specimens of the type species of each genus, however, differ in all holaspid instar stages (compare Figs 30 & 36), although less significantly in later ones. The early holaspid cephalon of *S. plicatus* is characterised by a relatively small anteroglabella and an extraordinarily long frontal sulcus, which penetrates to about the level of the F2 (see Fig. 36.1–6). Early holaspid instars of *Tomagnostus fissus* also have a frontal sulcus, but the anteroglabella is relatively large, its frontal sulcus is short, and the front part of its posteroglabella is tumid and carinate (see Fig. 30.6) rather than sulcate. Following a seemingly abrupt ontogenetic transformation, the frontal sulcus is entirely effaced from the middle holaspid cephalon of *S. plicatus*, and its anteroglabella is much enlarged in relative size (see Fig. 36.7a-c). In comparison, ontogenetic changes in proportions of the anteroglabella and length of the frontal sulcus are minor in *T. fissus.* These and other differences in axial structure are considered to have important taxonomic significance, and are the basis for distinguishing the new genus *Schismagnostus.* Based on all characters, but especially those of early ontogenetic stages, *Schismagnostus* does not seem to be closely related to any described agnostoid genus, and its phyletic origin is obscure.

Two species are here assigned or reassigned to *Schismagnostus.* One is the type species, *S. plicatus* n. sp., which is known from only the *Ptychagnostus gibbus* Zone of North Greenland. The other is *S. clarus* (Pokrovskaya & Egorova *in* Egorova *et al.*, 1982, p. 60, text-fig. 2, pl. 14, figs 7, 8), which has a reported range in Siberia corresponding to the interval from the lower *Ptychagnostus punctuosus* Zone to the lower *Lejopyge laevigata* Zone.

Schismagnostus plicatus n. sp.

Fig. 36

Etymology. Greek *plicatus*, folded; referring to the strong genal scrobiculae, even on the juvenile cephalon.

Holotype. Cephalon (Fig. 36.9a, b), MGUH 21.508 from GGU 298970.

Material. Nine cephala and 2 pygidia are in GGU 298970.

Diagnosis. Cephalon having extraordinarily long frontal sulcus on glabella of early holaspides, but effaced on later holaspides. Basal lobes exceptionally short. Pygidium with short axis, pleural fields divided by deep postaxial median furrow, and pair of large border spines.

Description. Cephalon ovate to subquadrate; anterior margin broadly rounded to nearly straight, lateral sides tapering rearward. Glabella bipartite with F3 bowed rearward. Frontal sulcus extraordinarily long in early holaspides, extending rearward to about level of F2; seemingly becoming abruptly effaced between early and middle holaspid stages. Anteroglabella short and laterally constricted in early holaspides, width being about half that of postjacent segment; abruptly increasing in relative size as frontal sulcus is effaced. Posteroglabella elongate rectangular; F2 weak to moderately well defined, F1 well defined; M3 laterally tumid, divided by frontal sulcus in early holaspides and by shallow depression in later holaspides; M2 may be slightly constricted and less tumid than M1 and M3 in early holaspides; M1 subcircular. Median glabellar node weak; shifting from front of M1 in early holaspides to middle M2 in later holaspides. Basal lobes extraordinarily reduced in length, being only slightly longer than exsaggital width of posterior border in early holaspides, gradually enlarging in later holaspides, but still exceptionally short in late holaspid stage. Genae having prominent scrobiculae throughout holaspid ontogeny; rugae becoming more complex during ontogeny, developing as many as five orders of branching in late holaspides. Border furrow and border both narrow.

Thorax not known.

Pygidium subquadrate with lateral sides tapering forward. Axis short, well separated from posterior border furrow; F1 shallow, bowed anteriorly; F2 shallow, straight or bowed forward; median tubercle on M2 ovate, moderately large, and most tumid toward rear; posteroaxis slightly ogival with shallow transverse sulcus containing median node surrounded by two pairs of tiny pits. Pleural fields having rough surface; divided by deep, median, postaxial furrow. Border furrow moderately wide. Border moderately wide posteriorly, narrowing anterolaterally; expanding posterolaterally into pair of large, broad-based spines.

Remarks. S. plicatus appears to be closely related to *Tomagnostus clarus* Egorova & Pokrovskaya (*in* Egorova *et al.*, 1982, p. 60, pl. 14, figs 7, 8), which is here reassigned to *Schismagnostus*. Late holaspid specimens of *S. plicatus* can easily be distinguished from those of *S. clarus,* however, by their distinctly shorter basal lobes, a shorter pygidial axis, presence of a postaxial median furrow, narrower pygidial border furrow, and larger pygidial border spines. Early holaspid specimens have not been described or illustrated for *S. clarus,* and therefore cannot be compared with those of *S. plicatus*.

Occurrence. All specimens of *S. plicatus* are from the middle Henson Gletscher Formation of Nyeboe Land, and are from the *Ptychagnostus gibbus* Zone.

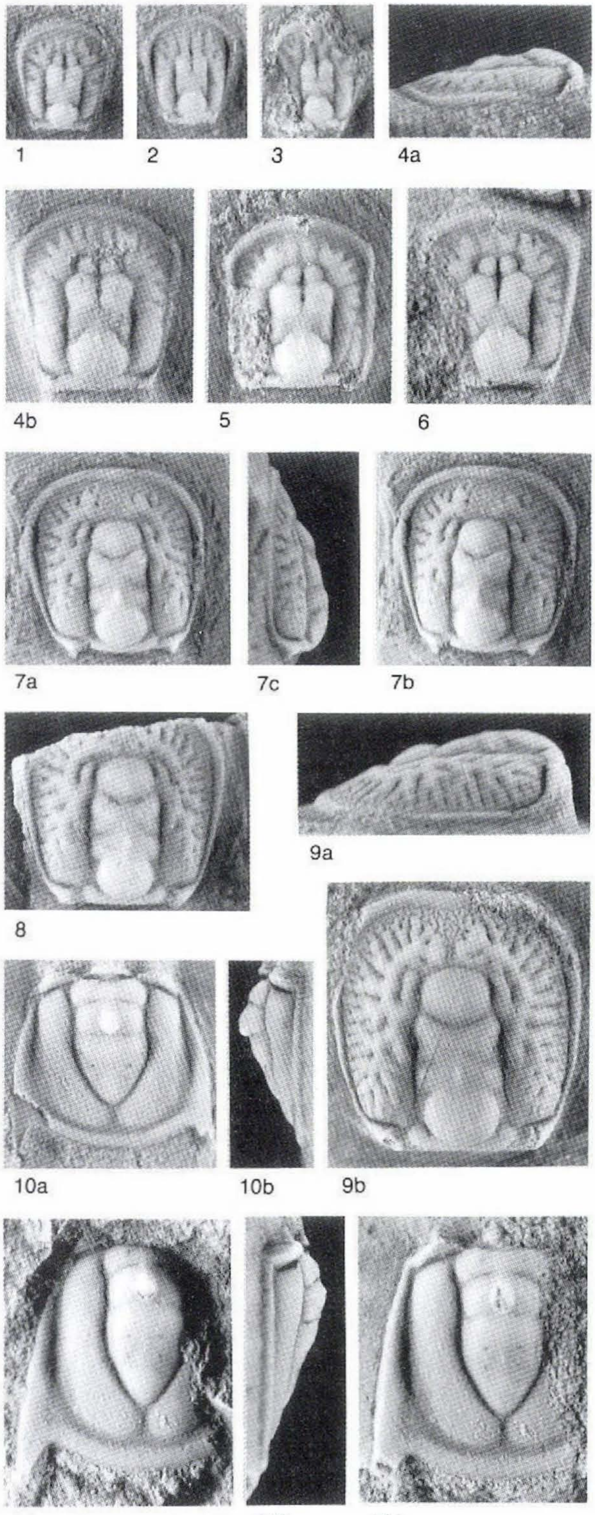


Fig. 36. *Schismagnostus plicatus* n. gen. & n. sp. All specimens are from GGU 298970. 1–3, late meraspid or early holaspid cephala, MGUH 21.500–21.502, all × 10. 4a, b, cephalon, probably an early holaspid, in lateral and dorsal views, MGUH 21.503, × 10. 5, 6, cephala, probably early holaspides, MGUH 21.504 and 21.505, both × 10. 7a-c, middle holaspid cephalon in stereographic (a, b) and lateral (c) views, MGUH 21.506, × 10. 8, incomplete middle holaspid cephalon, MGUH 21.507, × 10. 9a, b, holotype cephalon in lateral and dorsal views, MGUH 21.508, × 8. 10a, b, pygidium in dorsal and lateral views, MGUH 21.509, × 8. 11a-c, pygidium in lateral and dorsal views (b, c) and latex cast showing more complete right marginal spine (a), MGUH 21.510, × 8.

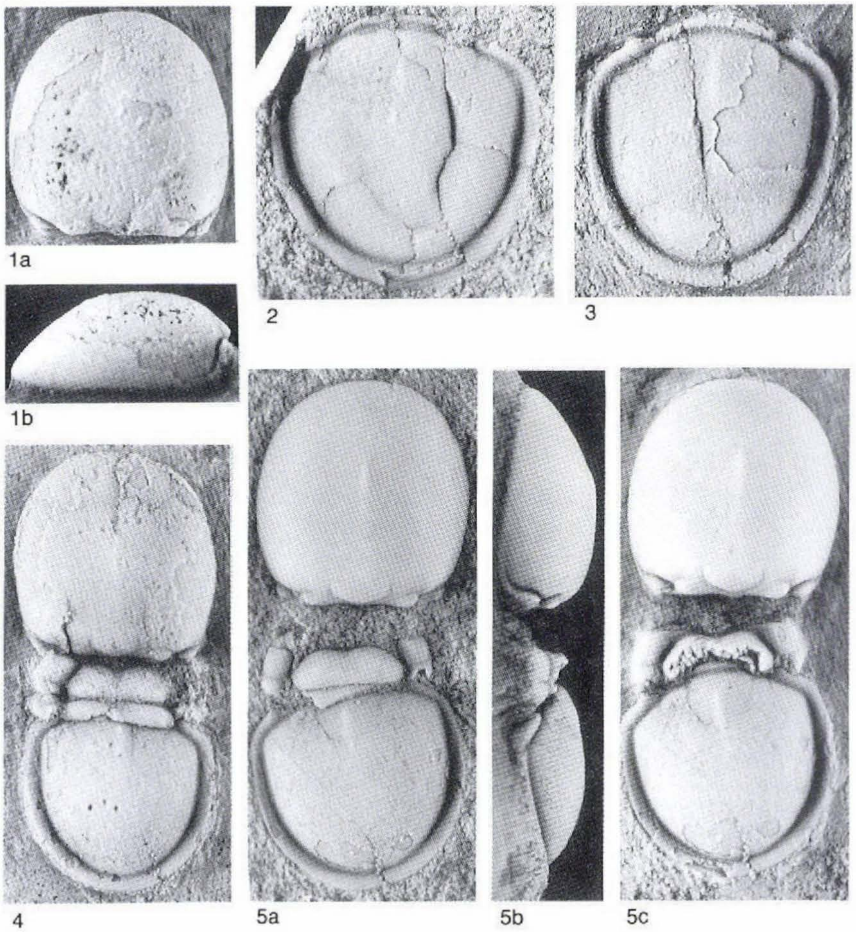


Fig. 37. *Toragnostus bituberculatus* (Angelin). 1a, b, cephalon in dorsal and lateral views, MGUH 21.511 from GGU 313115, × 8. 2, latex cast of pygidium with doublure exposed where posterior border is broken, MGUH 21.512 from GGU 313115, × 8. 3, flattened pygidium, MGUH 21.513 from GGU 301312, × 8. 4, dorsal exoskeleton, MGUH 21.514 from GGU 301313, × 10. 5a-c, dorsal exoskeleton, MGUH 21.515 from GGU 301313, all × 10; a, latex cast showing nearly complete anterior thoracic segment; b, c, specimen in lateral and dorsal views.

Genus *Toragnostus* Robison, 1988

Type species. Agnostus bituberculatus Angelin, 1851, p. 6.

Remarks. The generic diagnosis of Robison (1988, pp. 52–53) is followed here (see also Shergold *et al.*, 1990, p. 57).

Toragnostus bituberculatus (Angelin, 1851)

Fig. 37

New material. More than 70 specimens are in GGU 301312 (rare), 301313 (abundant), and 313115 (common).

Remarks. Complete specimens of *T. bituberculatus* in GGU 301313 (Fig. 37.4, 5) are the first to be illustrated for the species. These show the anterior thoracic segment to be longer sagittally than the posterior thoracic segment, and the axial ring of each thoracic segment is smooth. All new material, including numerous disarticulated cephala and pygidia, agrees well with previous descriptions of the species (for synonymy, see Robison, 1988, p. 53).

Lu & Lin (1989, pp. 113–114, 230, pl. 13, figs 7–10) named a new species *Phalagnostus carinatus* that appears to be conspecific with *T. bituberculatus*, but it is said to differ by having a longer and more posterior median carina on the cephalon as well as slight differences in the vestigial axial furrow and uniformity in width of the border on the pygidium. The three illustrated cephala of the Chinese species are not well preserved and the nature of the median carina is not clear from the photographs. Characters of the single illustrated pygidium appear to be within the range of variation observed elsewhere in populations of *T. bituberculatus*. Thus, I consider *P. carinatus* Lu & Lin to be a questionable junior synonym of *T. bituberculatus*.

Occurrence. T. bituberculatus is geographically widespread in the *Lejopyge laevigata* Zone. Rare specimens have been previously documented from the upper *L.*

laevigata Zone in the lower Holm Dal Formation of Peary Land, North Greenland (Robison, 1988, p. 53, fig. 12.4–6). The new specimens are from the lower *L. laevigata* Zone in basal beds of the Kap Stanton Formation of Peary Land.

Genus and species undetermined 1

Fig. 9.1a, b

Remarks. A single pygidium in GGU 298970 from the *Ptychagnostus gibbus* Zone of the middle Henson Gletscher Formation, Nyeboe Land, is unassigned to genus and species. It is characterised by a bowed articulating furrow, fully developed ring furrows (F1 & F2), a carinate median tubercle, a tumid and ogival posteroaxis, a short postaxial median furrow, a wide border furrow, and a pair of border spines. It resembles pygidia of *Peronopsis bulkurensis,* discussed above, but differs by having a bowed rather than straight articulating furrow and better developed ring furrows. It resembles *Schismagnostus plicatus* n. gen. & n. sp., described above, in development of ring furrows, but its posteroaxis is more tumid, it lacks a transverse sulcus, and its border spines are less robust. It also resembles pygidia of *Peronopsis segmenta* Robison, 1964 (compare Robison, 1982, pl. 6, figs 3, 4), but the F2 is not effaced.

Genus and species undetermined 2

Fig. 9.2, 3

Material. Two cephala are in GGU 298969 and one cephalon is in GGU 298970.

Remarks. Three small cephala of this taxon are characterised by a long, narrow, bipartite glabella with an F3 that is bowed slightly rearward. The glabella also has a short frontal sulcus. The posteroglabella is unusually long and its median node is posterior from the midpoint. Basal lobes are simple and do not indent the glabella, genae are smooth, and the border is moderately wide anteriorly and tapers posteriorly. Considering all characters, these cephala resemble those of *Tomagnostus* but the border is wider anteriorly and of less uniform width, and the basal lobes do not indent the glabella.

Occurrence. This taxon is from the upper Henson Gletscher Formation in Nyeboe Land, being present in both the *Ptychagnostus gibbus* and *Ptychagnostus atavus* zones.

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References

Ahlberg, P. 1988: A revision of the Ordovician agnostid trilobite *Leiagnostus* Jaekel 1909. *Geol. Fören. Stockholm Förh.* **110,** 363–370.

Ahlberg, P. 1992: Agnostid trilobites from the Lower Ordovician of southern Sweden. *Trans. R. Soc. Edinburgh* **83,** 539–570.

Angelin, N. P. 1851: *Palaeontologia Suecica, pars I: Iconographia crustaceorum formationis transitionis,* 24 pp. Lund: Weigel.

Babcock, L. E. 1994a: Systematics and phylogenetics of polymeroid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Bull. Grønlands geol. Unders.* **169** (this volume).

Babcock, L. E. 1994b: Biogeography and biofacies patterns of the Middle Cambrian polymeroid trilobites from North Greenland: palaeogeographic and palaeo-oceanographic implications. *Bull. Grønlands geol. Unders.* **169** (this volume).

Barrande, J. 1846: Notice préliminaire sur le Systême silurien et les Trilobites de Bohême, 96 pp. Leipzig: Hirschfeld.

Belt, T. 1868: On the 'Lingula Flags,' or 'Festiniog Group' of the Dolgelly district, part III. *Geol. Mag.* **5,** 5–11.

Bergeron, J. 1889: Étude géologique du Massif ancien situé au sud du plateau central. *Annales Sci. Géol., Paris* **22,** 361 pp.

Beyrich, E. 1845: *Ueber einige böhmische Trilobiten,* 47 pp. Berlin: G. Reimer.

Borovikov, L. T. & Kryskov, L. N. 1963: [Cambrian deposits of the Kendyktas Mountains (south Kazakhstan)]. *Trudy Vses. Nauch.-Issled. geol. Inst (VSEGEI), 1,* N S **94** [in Russian; not seen, cited by Öpik 1967].

Brøgger, W. C. 1878: Om paradoxideskifrene ved Krekling. *Nyt Mag. Naturvid.* **24,** 18–88.

Brongniart, A. 1822: Les Trilobites. *In* Brongniart, A. & Desmarest, A.-G., Histoire naturelle des crustacés fossiles, 1–66. Paris: F.-G. Levrault.

Chernysheva, N. E. (ed.) 1960: [*Principles of paleontology; arthropods, trilobites and crustaceans.*] Moscow: Gosudar. Nauchno-Tekh. Izd. Lit. Geol. Okhr. Nedr., 515 pp. (in Russian).

Courtessole, R. 1973: *Le Cambrien moyen de la Montagne Noire; biostratigraphie,* 248 pp. Toulouse: Lab. géol. CEARN, Fac. Sci.

Courtessole, R., Pillet, J. & Viscaino, D. 1988: Stratigraphie et paléontologie du Cambrien moyen greseux de la Montagne Noire (versant meridional). *Mém. Soc. d'Etudes Scientifiques de l'Aude, Carcassonne, France,* 55 pp.

Daily, B. & Jago, J. B. 1975: The trilobite *Lejopyge* Hawle & Corda and the Middle – Upper Cambrian boundary. *Palaeontology* **18,** 527–550.

Dalman, J. W. 1828: Nya Svenska Paleader. *Kongl. Sv. Vet.*

Acad., Årsberättelser om nyare zoologiska arbeten och upptäckter, 138 pp.

Dong Xiping 1990: A potential candidate for the Middle – Upper Cambrian boundary stratotype – an introduction to the Paibi section in Huayuan, Hunan. *Acta Geol. Sinica* **3,** 309–327.

Egorova, L. I., Xiang Liwen, Lee Shangi, Nan Ronshan & Kuo Zhengming 1963: [Cambrian trilobite fauna from Kwenchow and western Hunan.] *Stratigr. Palaeont.* **3**(1), 1–117. China Industrial Press, Beijing. (In Chinese.)

Egorova, L. I., Shabanov, Y. Y., Rozanov, A. Y., Savitsky, V. E., Chernysheva, N. E. & Shishkin, B. B. 1976: [Elansky and Kuonamsky facies stratotypes of the lower boundary of the Middle Cambrian in Siberia.] *Trudy Sibir. Nauchno-Issled. Inst. Geol. Geofiz. Miner. Syr.* **211,** 1–228 (in Russian).

Egorova, L. I., Shabanov, Y. Y., Pegel, T. V., Savitsky, V. E., Suchov, S. S. & Chernysheva, N. E. 1982: [Maya Stage of the type locality (Middle Cambrian of Siberian platform)]. *Trudy Akad. Nauk SSSR, Minist. Geol., Mezhbedom. Stratigr. Kom. SSSR* **8,** 1–146 (in Russian).

Ergaliev, G. K. 1980: [Middle and Upper Cambrian trilobites of the Lesser Karatau Range.] *Akad. Nauk Kazakh. SSR, Inst. Geol., Alma-Ata,* 210 pp. (in Russian).

Etheridge, R., Jr. 1902: Official contributions to the palaeontology of South Australia, no. 13; evidence of further Cambrian trilobites. *S. Aust. Parliamentary Pap.,* 3–4.

Fatka, O. & Kordule, V. 1992: New fossil sites in the Jince Formation (Middle Cambrian, Bohemia). *Věstník Českého geol. úst.* **67,** 47–60.

Fatka, O., Kordule, V. & Šnajdr, M. 1981: New Middle Cambrian trilobites from the Barrandian. *Věstník Ústřed. úst. geol.* **56,** 367–370.

Fortey, R. A. 1980: The Ordovician trilobites of Spitsbergen III: remaining trilobites of the Valhallfonna Formation. *Norsk Polarinstitutt Skr.* **171,** 163 pp.

Gil Cid, M. D. 1981: Los trilobites agnóstidos del Cámbrico Inferior y Medio de España. *Bol. Geol. Miner.* **92**(2), 21–36.

Grönwall, K. A. 1902: Bornholms Paradoxideslag og deres fauna. *Danm. geol. Unders.* (Ser. 2) **13,** 230 pp.

Gunther, L. F. & Gunther, V. G. 1981. Some Middle Cambrian fossils of Utah. *Brigham Young Univ. Geol. Studies* **28**(1), 81 pp.

Harrington, H. J. 1938: Sobre las faunas del Ordoviciano Inferior del norte Argentino. *Revta Mus. La Plata,* N S **1,** 109–289.

Harrington, H. J. *et al.* 1959: Trilobita. *In* Moore, R. C. (ed.) *Treatise on invertebrate paleontology, O, Arthropoda* **1,** O38–O560. Lawrence, Kansas: Geol. Soc. Am., Kansas Univ. Press.

Hartnoll, R. G. 1982: Growth. *In* Abele, L. G. (ed.) *The biology of Crustacea, volume 2, embryology, morphology, and genetics,* 111–196. New York: Academic Press.

Hawle, I. & Corda, A. J. C. 1847: Prodrom einer Monographie der böhmischen Trilobiten. *Abh. K. böhm. Ges. Wiss.* **5,** 176 pp.

Henningsmoen, G. 1958: The Upper Cambrian faunas of Norway. *Norsk geol. Tidsskr.* **38,** 179–196.

Hicks, H. 1872: On some undescribed fossils from the Menevian Group. *Q. Jl geol. Soc. Lond.* **28,** 173–185.

Holm, G. & Westergård, A. H. 1930: A Middle Cambrian fauna from Bennett Island. *Mem. Acad. Sci. l'URSS* **21**(8), 1–25.

Howell, B. F. 1925: The faunas of the Cambrian *Paradoxides* beds at Manuels, Newfoundland. *Bull. Am. Paleont.* **11**(43), 140 pp.

Howell, B. F. 1935a: New Cambrian agnostian trilobites from Vermont. *J. Paleont.* **9,** 218–221.

Howell, B. F. 1935b: Cambrian and Ordovician trilobites from Herault, southern France. *J. Paleont.* **9,** 222–238.

Howell, B. F. 1935c: Some New Brunswick Cambrian agnostians. *Bull. Wagner Free Inst. Sci.* **10**(2), 13–16.

Howell, B. F. 1937: Cambrian *Centropleura vermontensis* fauna of northwestern Vermont. *Bull. geol. Soc. Am.* **48,** 1147–1210.

Howell, B. F. 1955: *Phalagnostus,* new genus for trilobite *Battus nudus* Beyrich. *J. Paleont.* **29,** 925–926.

Hunt, A. S. 1966: Submarginal suture and ventral plate of an agnostid trilobite. *J. Paleont.* **40,** 1238–1240.

Hutchinson, R. D. 1962: Cambrian stratigraphy and trilobite faunas of southeastern Newfoundland. *Bull. geol. Surv. Can.* **88,** 156 pp.

Illing, V. C. 1916 [dated 1915]: Paradoxidian fauna of the Stokingford Shales. *Q. Jl geol. Soc. Lond.* **71,** 386–450.

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

Ineson, J. R., Surlyk, F., Higgins, A. K. & Peel, J. S. 1994: Slope apron and deep shelf sediments of the Brønlund Fjord and Tavsens Iskappe Groups (Lower Cambrian – Lower Ordovician), North Greenland: stratigraphy, facies and depositional setting. *Bull. Grønlands geol. Unders.* **169** (this volume).

Jaekel, O. 1909: Über die Agnostiden. *Z. dt. geol. Ges.* **61,** 380–401.

Jago, J. B. 1976: Late Middle Cambrian agnostid trilobites from north-western Tasmania. *Palaeontology* **19,** 133–172.

Jago, J. B. & Daily, B. 1974: The trilobite *Clavagnostus* Howell from the Cambrian of Tasmania. *Palaeontology* **17,** 95–109.

Jell, P. A. & Robison, R. A. 1978: Revision of a late Middle Cambrian trilobite faunule from northwestern Queensland. *Paleont. Contr. Univ. Kansas Pap.* **90,** 21 pp.

Khajrullina [Hairullina], T. I. 1970: [Trilobites of the Maiskov Stage of the Turkestan Mountains.] *In* Shayukuboe, T. S. (ed.) [*Biostratigraphy of the sedimentary area of Uzbekistan*] **9,** 5–53. Leningrad: Nedra (in Russian).

Khajrullina [Hairullina], T. I. 1973: [Biostratigraphy and trilobites of the Maiskov Stage, Middle Cambrian of the Turkestan Mountains]. *Sred-aziat. nauchno-issled. Inst. Geol. Miner. Syr. Tashkent: FAN,* 112 pp. (in Russian).

Khalfin, L. L. (ed.) 1960: [Paleozoic biostratigraphy of the Sayan-Altai mountain region, I; Lower Paleozoic]. *Trudy Sibir. Nauchno-Issled. Inst. Geol. Geofiz. Miner. Syr.* **19,** 1–498 (in Russian).

Kindle, C. H. 1982: The C. H. Kindle collection: Middle Cambrian to Lower Ordovician trilobites from the Cow Head

Group, western Newfoundland. *Pap. geol. Surv. Can.* **82–1C,** 1–17.

Kobayashi, T. 1937: The Cambro-Ordovician shelly faunas of South America. *J. Fac. Sci., Tokyo Univ.* **4**(4), 369–533.

Kobayashi, T. 1938: Upper Cambrian fossils from British Columbia with a discussion on the isolated occurrence of the so-called *Olenus* beds of Mt. Jubilee. *Japanese J. Geol. Geogr.* **15,** 149–192.

Kobayashi, T. 1939: On the agnostids (Part l). *J. Fac. Sci., Tokyo Univ.* **5**(5), 69–198.

Kobayashi, T. 1962: The Cambro-Ordovician formations and faunas of South Korea, part IX; palaeontology VIII, the Machari fauna. *J. Fac. Sci., Tokyo Univ.,* Sec. II, **14**(1), 1–152.

Lake, P. 1906: A monograph of the British Cambrian trilobites, part 1. *Monogr. Palaeontogr. Soc., London,* 1–28.

Lake, P. 1946: Monograph of the British Cambrian trilobites, part 14. *Monogr. Palaeontogr. Soc., London,* 333–350.

Laurie, J. R. 1988: Revision of some Australian Ptychagnostinae (Agnostida, Cambrian). *Alcheringa* **12,** 169–205.

Laurie, J. R. 1989: Revision of species of *Goniagnostus* Howell and *Lejopyge* Corda from Australia (Agnostida, Cambrian). *Alcheringa* **13,** 175–191.

Laurie, J. R. 1990: On the Middle Cambrian agnostoid species *Agnostus fallax* Linnarsson 1869. *Alcheringa* **14,** 317–324.

Lermontova, E. V. 1940: [Arthropoda.] *In* Vologdin, A. (ed.), [*Atlas of the leading forms of the fossil faunas of the USSR*] **1,** 112–157. Moscow-Leningrad: Gos. Izdat. Geol. Lit. (in Russian).

Lindström, G. 1901: Researches on the visual organs of the trilobites. *K. Svenska Vetensk.-Akad. Handl.* **34,** 1–87.

Linnarsson, J. G. O. 1869: Om Vestergötlands Cambriska och Siluriska aflagringar. *K. Svenska Vetensk.-Akad. Handl.* **8**(2), 1–89.

Linnarsson, J. G. O. 1879: Om faunan i kalken med *Conocoryphe exsulans* ('Coronatuskalken'). *Sver. geol. Unders.* **C 35,** 1–31.

Linnarsson, J. G. O. 1883 [dated 1882]: De undre Paradoxideslagren vid Andrarum. *Sver. geol. Unders.* **C 54,** 1–48.

Lu Yen-hao 1957: [Trilobita.] *In* [*Index fossils of China, Invertebrata*] **3,** 249–294. Peking: Geological Press (in Chinese).

Lu Yen-hao, Chang Wen-tang, Chu Chao-ling, Chien Yi-yuan & Hsiang Lee-wen 1965: [*Fossils of each group of China; Chinese trilobites.*] Vol. 1, 1–362; vol. 2, 363–766. Peking: Science Publication Company (in Chinese).

Lu Yanhao & Lin Huanling 1989: [The Cambrian trilobites of western Zhejiang.] *Palaeont. Sin.* **178**(N S B, 25), 1–287 (in Chinese with English summary).

M'Coy, F. 1849: On the classification of some British fossil Crustacea, with notices of new forms in the university collection at Cambridge. *Ann. Mag. Nat. Hist.* (London), ser. 2, **4,** 161–179, 392–414.

Matthew, G. F. 1896: Faunas of the *Paradoxides* beds in eastern North America, no. 1. *Trans. New York Acad. Sci.* **15,** 192–247.

Matthew, G. F. 1899: Studies on Cambrian faunas, no. 3; Upper Cambrian fauna of Mount Stehphen, British Columbia. *Trans. R. Soc. Canada,* ser. 2, **5**(4), 39–66.

Morris, S. F. 1988: A review of British trilobites, including a a synoptic revision of Salter's monograph. *Monogr. Palaeontogr. Soc.,* London **140**(574), 316 pp.

Morris, S. F. & Fortey, R. A. 1985: *Catalogue of the type and figured specimens of Trilobita in the British Museum (Natural History),* 183 pp. London: British Museum (Natural History).

Müller, K. J. & Walossek, D. 1987: Morphology, ontogeny, and life habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden. *Fossils & Strata* **19,** 124 pp.

Murphy, M. A. 1977: On time-stratigraphic units. *J. Paleont.* **51,** 213–219.

Nicholas, T. C. 1916 [dated 1915]: Notes on the trilobite fauna of the Middle Cambrian of the St. Tudwal's Peninsula (Carnarvonshire). *Q. Jl geol. Soc. Lond.* **71,** 451–472.

Nikolaisen, F. & Henningsmoen, G. 1990: Lower and Middle Cambrian trilobites from the Digermul Peninsula, Finnmark, northern Norway. *Norsk geol. Unders. Bull.* **419,** 55–95.

Öpik, A. A. 1961: The geology and palaeontology of the headwaters of the Burke River, Queensland. *Bur. Miner. Resour. Aust. Bull.* **53,** 249 pp.

Öpik, A. A. 1967: The Mindyallan fauna of north-western Queensland. *Bur. Miner. Resour. Aust. Bull.* **74,** vol. 1, 404 pp.; vol. 2, 167 pp., 67 pls.

Öpik, A. A. 1979: Middle Cambrian agnostids: systematics and biostratigraphy. *Bur. Miner. Resour. Aust. Bull.* **172,** vol. 1, 188 pp.; vol. 2, 67 pls.

Palmer, A. R. 1962: *Glyptagnostus* and associated trilobites in the United States. *U.S. geol. Surv. Prof. Pap.* **374F,** 49 pp.

Palmer, A. R. 1968: Cambrian trilobites of east-central Alaska. *U.S. geol. Surv. Prof. Pap.* **559B,** 115 pp.

Pek, I. & Vaněk, J. 1971: Revision of the genera *Peronopsis* Hawle et Corda, 1847 and *Diplorrhina* Hawle et Corda, 1847 (Trilobita) from the Middle Cambrian of Bohemia. *Věstník Ústřed. Úst. geol.* **46,** 269–275.

Pokrovskaya, N. V. 1958: [Middle Cambrian agnostids of Yakutia, part I.] *Trudy Geol. Inst., Akad. Nauk SSSR* **16,** 1–96 (in Russian).

Poulsen, C. 1960: Fossils from the late Middle Cambrian *Bolaspidella* Zone of Mendoza, Argentina. *Mat.-fys. Medd. Danske Vid. Selsk.* **32,** 42 pp.

Poulsen, V. 1966: Cambro-Silurian stratigraphy of Bornholm. *Meddr dansk geol. Foren.* **16,** 117–137.

Poulsen, V. 1969: An Atlantic Middle Cambrian fauna from North Greenland. *Lethaia* **2,** 1–14.

Poulsen, V. & Anderson, M. M. 1975: The Middle – Upper Cambrian transition in southeastern Newfoundland, Canada. *Can. J. Earth Sci.* **12,** 2065–2079.

Qiu Hong-an *et al.* 1983: [Trilobita.] *In* Nanjing Inst. Miner. Resour. [*Paleontological atlas of east China; vol. I, early Paleozoic*], 28–254. Beijing: Geological Publishing House (in Chinese).

Rasetti, F. 1948: Middle Cambrian trilobites from the conglomerates of Quebec. *J. Paleont.* **22,** 315–339.

Rasetti, F. 1967: Lower and Middle Cambrian trilobite faunas from the Taconic sequence of New York. *Smithson. misc. Collns* **152**(4), 111 pp.

Rasetti, F. & Theokritoff, G. 1967: Lower Cambrian agnostid trilobites of North America. *J. Paleont.* **41,** 189–196.

Repina, L. N., Petrunina, Z. E. & Khajrullina, T. I. 1975: [Trilobites.] *In* Repina, L. N. *et al.*, [Stratigraphy and fauna of the lower Paleozoic of the northern submontane belt of Turkestan and the Alai ridges (southern Tian Shan).] *Trudy Inst. Geol. Geofiz., Akad. Nauk SSSR, Sibir. Otdel.* **278,** 100–233 (in Russian).

Resser, C. E. 1939: The Spence Shale and its fauna. *Smithson. misc. Collns* **97**(12), 29 pp.

Resser, C. E. & Howell, B. F. 1938: Lower Cambrian *Olenellus* Zone of the Appalachians. *Bull. geol. Soc. Am.* **49,** 195–248.

Robison, R. A. 1964: Late Middle Cambrian faunas from western Utah. *J. Paleont.* **38,** 510–566.

Robison, R. A. 1972a: Hypostoma of agnostid trilobites. *Lethaia* **5,** 239–248.

Robison, R. A. 1972b: Mode of life of agnostid trilobites. *Proc. 24 int. geol. Congr. Montreal* **7,** 33–40.

Robison, R. A. 1976: Middle Cambrian trilobite biostratigraphy of the Great Basin. *Geol. Stud. Brigham Young Univ.* **23**(2), 93–109.

Robison, R. A. 1978: Origin, taxonomy, and homeomorphs of *Doryagnostus* (Cambrian Trilobita). *Paleontol. Contr. Univ. Kansas Pap.* **91,** 10 pp.

Robison, R. A. 1982: Some Middle Cambrian agnostoid trilobites from western North America. *J. Paleont.* **56,** 132–160.

Robison, R. A. 1984: Cambrian Agnostida of North America and Greenland; part I, Ptychagnostidae. *Paleontol. Contr. Univ. Kansas Pap.* **109,** 59 pp.

Robison, R. A. 1987: Class Trilobita. *In* Boardman, R. S. *et al.* (ed.) *Fossil invertebrates*, 221–241. Palo Alto, California: Blackwell.

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

Robison, R. A. 1991: Middle Cambrian biotic diversity: examples from four Utah lagerstatten. *In* Simonetta, A. M. & Conway Morris, S. (ed.) *The early evolution of metazoa and the significance of problematic taxa,* 77–98. Cambridge: Cambridge Univ. Press.

Robison, R. A. & Pantoja-Alor, J. 1968: Tremadocian trilobites from the Nochixtlan region, Oaxaca, Mexico. *J. Paleont.* **42,** 767–800.

Rosova, A. V. 1964: [Biostratigraphy and description of trilobites of the Middle and Upper Cambrian of the northwestern Siberian platform.] *Inst. Geol. Geofiz., Akad. Nauk SSSR, Sibir. Otdel.,* 1–148 (in Russian).

Rosova, A. V. 1977: [Upper Cambrian and Lower Ordovician of the Rubnoi, Khartaiki, Kureiki and Letnei river basins.] *In* Chernysheva, N. E. & Rosova, A. V. (ed.) [Biostratigraphy and fauna of the Upper Cambrian and its boundary layers.] *Trudy Inst. Geol. Geofiz., Adad. Nauk SSSR, Sibir. Otdel.* **313,** 54–84 (in Russian).

Rowell, A. J., Robison, R. A. & Strickland, D. K. 1982: Aspects of Cambrian agnostoid phylogeny and chronocorrelation. *J. Paleont.* **56,** 161–182.

Rushton, A. W. A. 1978: Fossils from the Middle – Upper Cambrian transition in the Nuneaton district. *Palaeontology* **21,** 245–283.

Rushton, A. W. A. 1979: A review of the Middle Cambrian Agnostida from the Abbey Shales, England. *Alcheringa* **3,** 43–61.

Rushton, A. W. A. 1983: Trilobites from the Upper Cambrian *Olenus* Zone in central England. *Spec. Pap. Paleontology* **30,** 107–139.

Salter, J. W. 1864: A monograph of the British trilobites from the Cambrian, Silurian, and Devonian formations. *Monogr. Palaeontogr. Soc., London,* 80 pp.

Samson, S., Palmer, A. R., Robison, R. A. & Secor, D. T. 1990: Biogeographical significance of Cambrian trilobites from the Carolina slate belt. *Bull. geol. Soc. Am.* **102,** 1459–1470.

Savitsky, V. E., Evtushenko, V. M., Egorova, L. I., Kontorovich, A. E. & Shabanov, Yu. Ya. 1972: [Cambrian of the Siberian platform (Judomian–Olenetsky type section, Kuonamsky Complex deposits).] *Trudy Sibir. Nauchno-Issled. Inst. Geol. Geofiz. Miner. Syr.* **130,** 1–200 (in Russian).

Sdzuy, K. 1961: Teil II: Trilobiten. *In* Lotze, F. & Sdzuy, K.: Das Kambrium Spaniens. *Abh. Akad. Wiss. Lit. Mainz, Abh. math.-naturwiss. Kl.* **7,** 499–594.

Shaw, A. B. 1966: Paleontology of northwestern Vermont. XI. Fossils from the Middle Cambrian St. Albans Shale. *J. Paleont.* **40,** 843–858.

Shergold, J. H. 1982: Idamean (Late Cambrian) trilobites, Burke River structural belt, western Queensland. *Bur. Miner. Resour. Austr. Bull.* **187,** 103 pp.

Shergold, J. H. & Laurie, J. R. 1991: *Ptychagnostus* Jaekel, 1909 and *Glyptagnostus* Whitehouse, 1936 (Trilobita): proposed conservation of accepted usage. *Bull. Zool. Nomenclature* **48**(3), 200–202.

Shergold, J. H., Laurie, J. R. & Sun Xiaowen 1990: Classification and review of the trilobite order Agnostida Salter, 1864: an Australian perspective. *Bur. Miner. Resour. Aust. Rep.* **296,** 93 pp.

Šnajdr, M. 1957: O novych trilobitech z ceskeho kambria. *Věstník Ústřed. Úst. geol.* **32,** 235–244.

Šnajdr, M. 1958: Trilobiti českého středního kambria. *Rospravy Ústřed. Úst. geol.* **24,** 1–280.

Song Yanping 1989: Upper Middle Cambrian trilobite biostratigraphy of western Hunan, China. Unpublished M.S. thesis, Univ. Kansas, Lawrence, 75 pp.

Sun Xiaowen 1989: Cambrian agnostids from the north China platform. *Palaeontol. Cathayana* **4,** 53–129.

Swofford, D. L. 1990: *PAUP: phylogenetic analysis using parsimony, version 3.0,* 35 pp. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Tullberg, S. A. 1880: Om *Agnostus*-arterna i de Kambriska aflagringarne vid Andrarum. *Sver. geol. Unders.* **C 42,** 37 pp.

Wahlenberg, G. 1818: Petrificata telluris Svecanae. *Nova Acta R. Soc. Sci. Upsala* **8,** 116 pp.

Walossek, D. & Müller, K. J. 1990: Upper Cambrian stem-lineage crustaceans and their bearing upon the monophyletic origin of Crustacea and the position of *Agnostus. Lethaia* **23,** 409–427.

Wang Shuei *et al.* 1963: [*Handbook of fossils, northwestern China*], 179 pp. Peking: Science Press, Academia Sinica (in Chinese).

Westergård, A. H. 1936: *Paradoxides oelandicus* beds of Öland. *Sver. geol. Unders.* **C 394,** 66 pp.

Westergård, A. H. 1946: Agnostidea of the Middle Cambrian of Sweden. *Sver. geol. Unders.* **C 477,** 141 pp.

Westergård, A. H. 1947: Supplementary notes on the Upper Cambrian trilobites of Sweden. *Sver. geol. Unders.* **C 489,** 35 pp.

White, C. A. 1874: Preliminary report upon invertebrate fossils, with descriptions of new species. *U.S. geol. Exploration West 100th Meridian* [Wheeler Survey], pamphlet, 27 pp.

Whitehouse, F. W. 1936: The Cambrian faunas of north-eastern Australia, parts 1 and 2. *Mem. Queensland Mus.* **11,** 59–112.

Whitehouse, F. W. 1939: The Cambrian faunas of north-eastern Australia, Part 3. *Mem. Queensland Mus.* N S **1,** 179–282.

Williamson, D. I. 1982: Larval morphology and diversity. *In* Abele, L. G. (ed.) *The biology of Crustacea.* Vol. 2, *Embryology, morphology, and genetics,* 43–110. New York: Academic Press.

Xiang Liwen & Zhang Tai-rong 1985: [Systematic descriptions of trilobites.] *In* [Stratigraphy and trilobite faunas of the Cambrian in the western part of the northern Tian Shan, Xinjiang.] *Minist. Geol. Miner. Resour., Geol. Mem.* **2**(4), 64–243 (in Chinese with English summary).

Xiang Liwen *et al.* 1981. [The Cambrian System of China.] *Chinese Acad. Geol., Stratig. China* **4,** 210 pp. (in Chinese).

Yang Jia-lu 1978: [Middle and Upper Cambrian trilobites of western Hunan and eastern Guizhou.] *Chinese Acad. Geol. Sci., Prof. Pap. Stratigr. Paleont.* **4,** 1–82 (in Chinese).

Yang Jia-lu 1982: [Notes on the Middle Cambrian trilobite faunas from Duibian of Jiangshan, Zhejiang.] *Geol. Rev.* **28**(4), 299–307 (in Chinese with English abstract).

Young, G. A. & Ludvigsen, R. 1989: Mid-Cambrian trilobites from the lowest part of the Cow Head Group, western Newfoundland. *Bull. geol. Surv. Can.* **392,** 49 pp.

Zhang Yu-song (ed.) 1983: [*Paleontological atlas of east China; part 1, early Paleozoic.*] Nanjing Inst. Geol. Miner. Resour., 657 pp. Beijing: Geol. Publishing House (in Chinese).

Zhang Wentang & Jell, P. A. 1987: *Cambrian trilobites of north China; Chinese Cambrian trilobites housed in the Smithsonian Institution,* 459 pp. Beijing: Science Press.

Zhou Tien-mei, Liu Yi-jeng, Mong Sien-sung & Sun Zheng-hua 1977: [Trilobita.] *In* Wang Xiao-feng & Jin Yu-qin (ed.) [*Palaeontological handbook of central and southern China; part I, early Palaeozoic Era*], 104–266. Beijing: Sciences Press (in Chinese).

Systematics and phylogenetics of polymeroid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland

Loren E. Babcock

Middle Cambrian strata of northernmost North Greenland contain polymeroid trilobites of Laurentian and Baltic aspect. Trilobites of Laurentian aspect were found primarily in lime mudstone and wackestone representing shelf lithofacies, whereas trilobites of Baltic aspect were found primarily in lime mudstone representing outer shelf lithofacies. Rare packstone beds in the deeper water lithofacies contain assemblages of mixed aspect.

Thirty-three polymeroid species, some in open nomenclature, are described from the Henson Gletscher and Kap Stanton formations of Nyeboe Land and Peary Land. Of the 21 genera identified, one eodiscid, *Costadiscus*, is new. Six species, *Bathyuriscus concavus*, *Costadiscus minutus*, *Dasometopus groenlandicus*, *Elyx trapezoidalis*, *Kootenia nodosa*, and *Opsidiscus longispinus*, are new.

Cladistic analysis indicates that eodiscid trilobites are a paraphyletic and possibly polyphyletic group that probably arose from polymeroid ancestors through mosaic heterochrony. The Polymerida, as previously applied, is also interpreted to be a paraphyletic group. Small size in eodiscids was achieved independently from that in agnostoids and condylopygids, probably through progenesis. Loss of eyes in some eodiscids evidently occurred in more than one evolutionary lineage. Available evidence suggests that agnostoids and eodiscids did not share a close common ancestor.

Cladistic analysis of *Xystridura*, *Galahetes*, *Lermontovia*, *Bergeroniellus*, *Paradoxides*, *Anopolenus*, *Clarella*, and *Centropleura* indicates that these trilobites are part of one monophyletic group, the family Paradoxididae. Two smaller clades within the Paradoxididae are recognised; these are the subfamilies Xystridurinae, with *Xystridura* and *Galahetes*, and Paradoxidinae with all the other paradoxidid genera. Both paedomorphic and peramorphic processes are inferred to have been important in the evolution of the paradoxidid trilobites.

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New occurrences of Middle Cambrian polymeroid trilobites from the Henson Gletscher and Kap Stanton formations of Nyeboe Land, and the Kap Stanton Formation of Peary Land, North Greenland (Fig. 1), are documented here. Trilobites from these areas were collected by staff of the Geological Survey of Greenland (GGU) and are relatively abundant and diverse (Table 1). The biofacies and biogeographic significance of these trilobites, and their implications for palaeo-oceanographic and plate-tectonic reconstructions are addressed in an accompanying paper (Babcock, 1994). Some of the fossils described here were the basis for preliminary studies by Fletcher *et al.* (1988), Babcock & Robison (1989), and Robison & Babcock (1990). Collections range in age from the *Glossopleura* Biochron to the *Lejopyge laevigata* Biochron. Trilobites from the *Glossopleura* Assemblage-zone are entirely polymeroids, whereas those from the *Ptychagnostus gibbus*, *P. atavus*, and *Lejopyge laevigata* interval-zones are mixed polymeroids and agnostoids. The agnostoid trilobites are described in an accompanying paper (Robison, 1994).

Middle Cambrian strata of North Greenland contain polymeroid trilobites of both Laurentian and Baltic aspect. Most previously described polymeroids are of Laurentian aspect (Poulsen, 1927; Poulsen, 1964; Palmer & Peel, 1981; Robison, 1988), which accords with the interpretation (Scotese *et al.*, 1979; Scotese & McKerrow, 1990) that Greenland and North America were united in a single Cambrian continent, Laurentia (see also Peel & Christie, 1982; Higgins *et al.*, 1991). Taxa of Baltic

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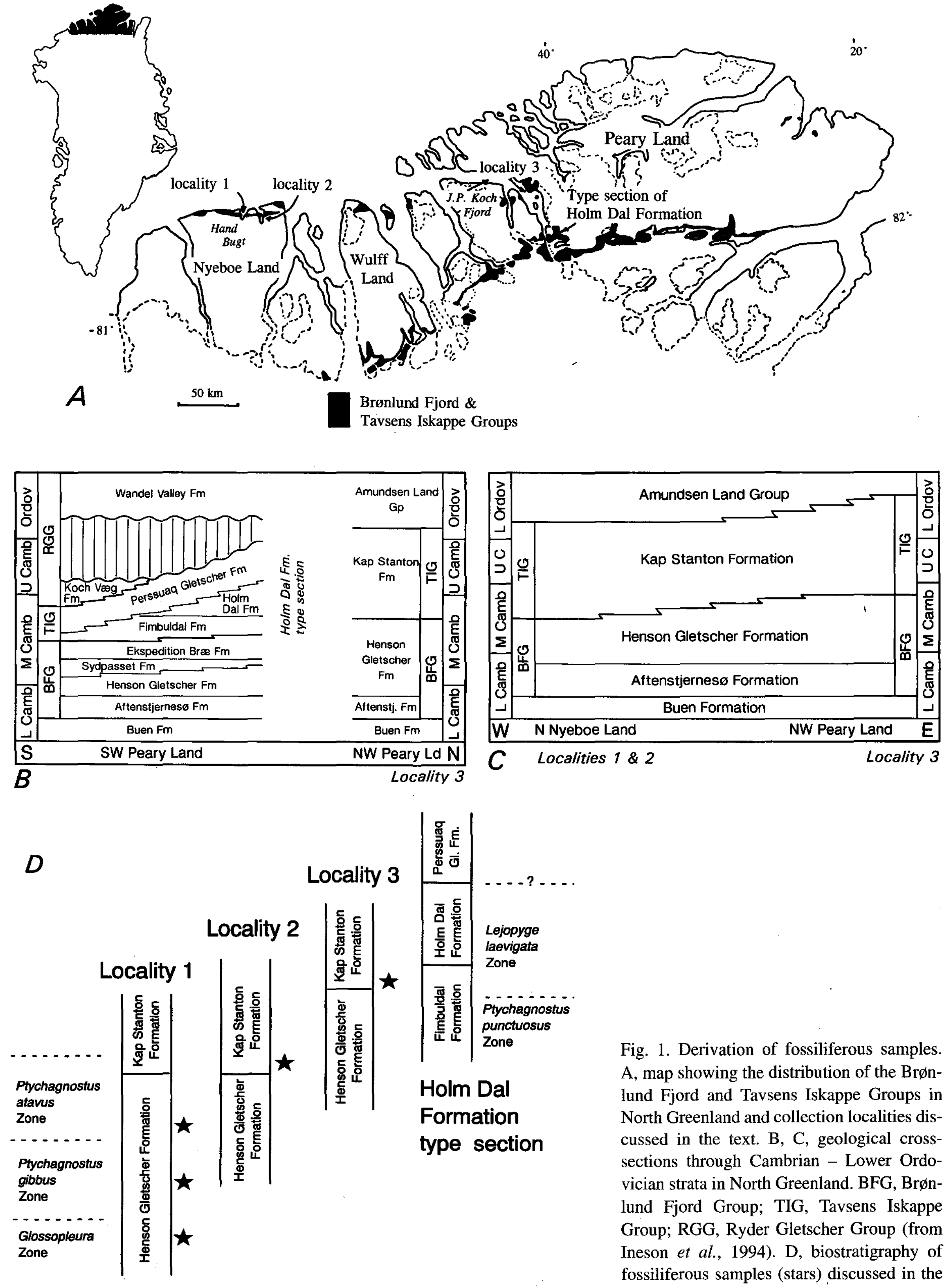


Fig. 1. Derivation of fossiliferous samples. A, map showing the distribution of the Brønlund Fjord and Tavsens Iskappe Groups in North Greenland and collection localities discussed in the text. B, C, geological cross-sections through Cambrian – Lower Ordovician strata in North Greenland. BFG, Brønlund Fjord Group; TIG, Tavsens Iskappe Group; RGG, Ryder Gletscher Group (from Ineson *et al.*, 1994). D, biostratigraphy of fossiliferous samples (stars) discussed in the text.

aspect are present along the northern coast of Greenland in Nyeboe Land and Peary Land (Poulsen, 1969; Fletcher *et al.*, 1988; Babcock & Robison, 1989; Babcock, 1990a; Robison & Babcock, 1990). Although polymeroids of Baltic aspect have been previously described from autochthonous or parautochthonous rocks of Laurentia (Howell, 1937; Hutchinson, 1952; Shaw, 1966; Rasetti, 1967; Palmer & Stewart, 1968; Babcock, 1990a), new specimens from North Greenland are the first from relatively undisturbed stratigraphic sequences. Polymeroids described here (Table 1) and associated agnostoids described by Robison (1994) are preserved in shelf lithofacies that represent native terranes (as defined by Keppie, 1989) of the Laurentian palaeocontinent. This new material significantly increases the record of Cambrian trilobites from the Innuitian margin of Laurentia.

Together with taxa described recently from the upper Middle Cambrian Holm Dal Formation (Robison, 1988), the new material provides important new data on the biogeography of Middle Cambrian trilobites. Differences between Middle Cambrian polymeroid assemblages of Laurentian and Baltic aspect are inferred to have been controlled by, or covaried with, water temperature and are not necessarily due to endemism developed around distantly separated cratons (Babcock, 1994).

Geologic setting and stratigraphy

Lower Palaeozoic rocks crop out along the coast of North Greenland in a band up to 250 km wide, forming the continuation of the Franklinian Basin of the Canadian Arctic Islands (Higgins *et al.*, 1991; Surlyk, 1991). The northernmost part of this outcrop belt lies within the east–west trending North Greenland fold belt, which consists of Upper Proterozoic? to Silurian sedimentary rocks that were deformed and metamorphosed primarily during the Ellesmerian orogeny of Devonian age (Dawes, 1971, 1976; Dawes & Soper, 1973; Higgins *et al.*, 1981, 1991; Surlyk, 1991). Localised structural overprinting occurred during the Eurekan orogeny of Cretaceous to Tertiary age (Dawes, 1971, 1976; Higgins *et al.*, 1981; Surlyk, 1991). The North Greenland fold belt is a continuation of the Innuitian orogenic system of arctic Canada (Dawes, 1976; Higgins *et al.*, 1991).

The stratigraphy and evolution of the Cambrian shelf, slope, and basin in North Greenland have been discussed by Ineson (1980, 1985, 1988), Ineson & Peel (1987, unpublished), Peel (1982), Peel & Christie (1982), Surlyk & Ineson (1987), Higgins *et al.* (1991), Surlyk (1991), and a summary by Ineson *et al.* (1994) is published together with this paper.

Table 1. Classification of polymeroid trilobites identified from the Henson Gletscher and Kap Stanton formations

'Polymerida'
- Family Anomocaridae
  - *Anomocarina excavata* (Angelin)
- Family Conocoryphidae
  - *Dasometopus groenlandicus* n. sp.
  - *Elyx trapezoidalis* n. sp.
  - *Hartshillia inflata* (Hicks)
- Family Corynexochidae
  - *Corynexochus*? sp.
- Family Dolichometopidae
  - *Bathyuriscus concavus* n. sp.
  - *Bathyuriscus* sp.
  - *Glossopleura walcotti* Poulsen
- Family Dorypygidae
  - *Kootenia nodosa* n. sp.
  - *Olenoides* sp.
  - *Olenoides* cf. *O. convexus* Rasetti
- Family Menomoniidae
  - *Bolaspidella* sp.
- Family Ogygopsidae
  - *Ogygopsis klotzi* (Rominger)
- Family Paradoxididae
  - *Centropleura loveni* (Angelin)
  - *Centropleura angelini*? Westergård
- Family Solenopleuridae
  - *Parasolenopleura aculeata* (Angelin)
  - *Solenopleura bucculenta* Grönwall
  - *Solenopleurella transversa*? Rasetti
- Family Zacanthoididae
  - *Zacanthoides* sp.
- Family unassigned
  - *Elrathia* sp.
  - *Syspacephalus* sp. 1
  - *Syspacephalus* sp. 2
  - *Syspacephalus* sp. 3
  - *Eodiscus scanicus* (Linnarsson)
  - *Costadiscus minutus* n. gen., n. sp.
  - *Opsidiscus longispinus* n. sp.
  - Undetermined corynexochoid
  - Undetermined ptychoparioid 1
  - Undetermined ptychoparioid 2
  - Undetermined ptychoparioid 3
  - Undetermined ptychoparioid 4
  - Undetermined ptychoparioid 5
  - Undetermined ptychoparioid 6

Two major depositional environments are represented by Cambrian rocks of North Greenland (Higgins *et al.*, 1991; Ineson *et al.*, 1994). An extensive carbonate shelf lay to the south in the area near the margin of the present-day Inland Ice, and a deeper water trough was in an area

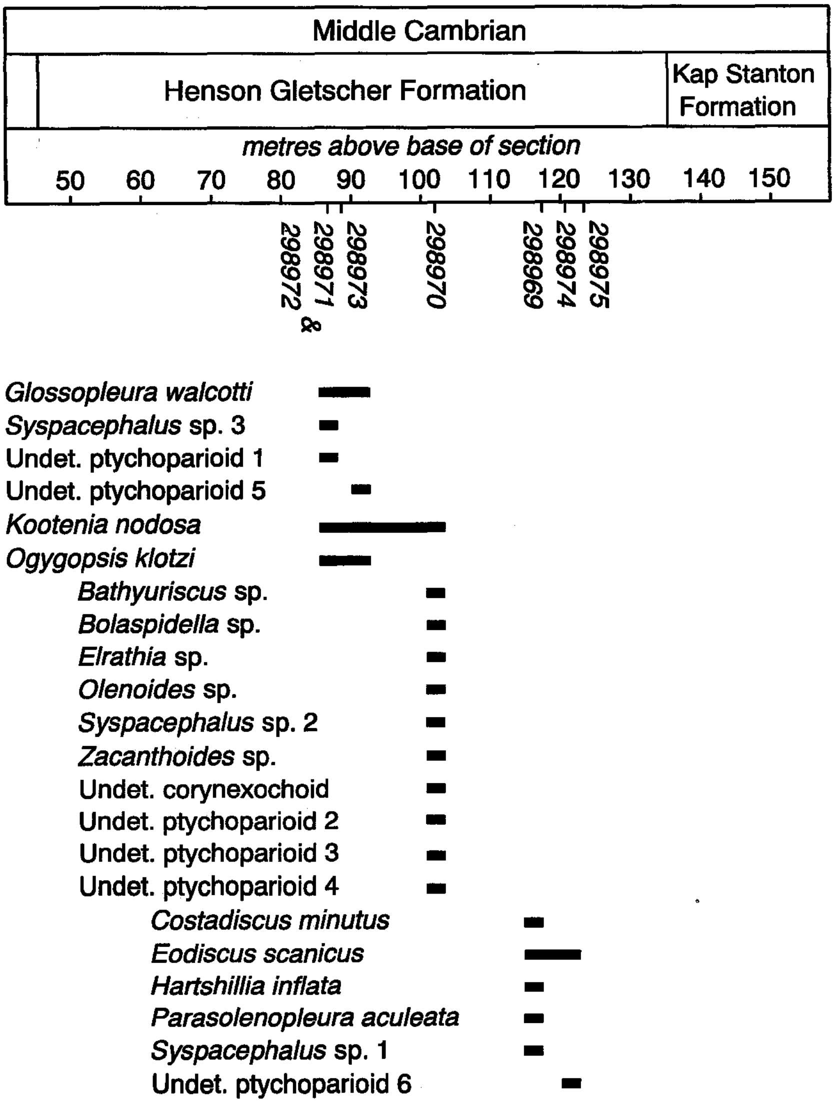


Fig. 2. Stratigraphic distribution of polymeroid trilobites in GGU collections from the Henson Gletscher Formation in Hand Bugt, Nyeboe Land (locality 1, Fig. 1). The base of the Henson Gletscher Formation is 46 m above the base of the measured section. GGU collections 298971 to 298973 are from the *Glossopleura* Assemblage-zone; GGU collection 298970 is from the *Ptychagnostus gibbus* Interval-zone; and GGU collections 298969, 298974, and 298975 are from the *Ptychagnostus atavus* Interval-zone.

to the present-day north. The relationship between the shelf and trough was complex, with the margin being largely fault controlled. Cambrian shelf deposits reach a maximum thickness of about 1.5 km and the basinal deposits are 2 to 3 km thick.

Rocks containing trilobites reported here have been only moderately disrupted structurally (Fletcher *et al.*, 1988; also see Soper & Higgins, 1985; Higgins *et al.*, 1991). Stratigraphic relationships show that they were deposited mainly in outer shelf environments. Correlation of strata containing the fossils described herein along well-exposed fjord walls to undeformed sequences in the south, deposited higher on the shelf, indicates that these outer shelf rocks are autochthonous, not allochthonous (Higgins *et al.*, 1991; Ineson *et al.*, 1994). Palaeontologic evidence, in the form of mixed assemblages of trilobites from warm-water and cool-water biofacies near the shelf margin (Babcock, 1991, 1994), supports that interpretation.

Lithostratigraphy and fossil localities

New polymeroid trilobites have been collected from two localities in Nyeboe Land and one in Peary Land, North Greenland (Fig. 1). Collections were obtained from the middle and upper parts of the Henson Gletscher Formation of the Brønlund Fjord Group and the basal beds of the Kap Stanton Formation of the Tavsens Iskappe Group, which locally overlies the Henson Gletscher Formation (Fig. 1).

The Kap Stanton Formation is formally defined in an

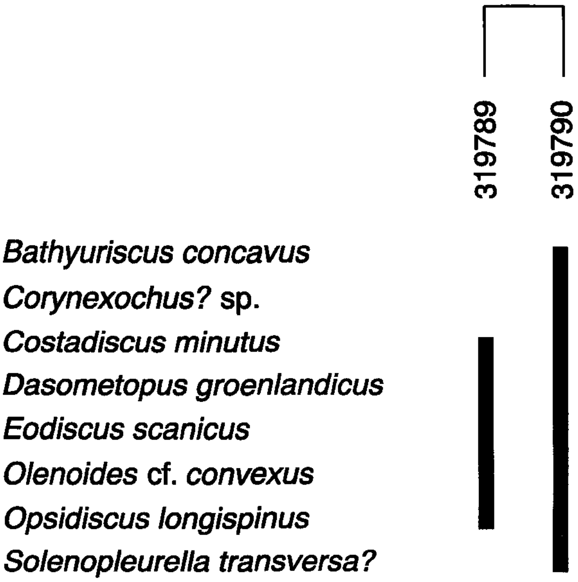


Fig. 3. Polymeroid trilobites in GGU collections from basal beds of the Kap Stanton Formation on the east side of Frankfield Bugt, Nyeboe Land (locality 2, Fig. 1). Collections are from the lower part of the *Ptychagnostus atavus* Interval-zone.

accompanying paper by Ineson *et al.* (1994), who also present a general description of the geologic environment. The Henson Gletscher Formation in southern Freuchen Land contains trilobites of Early to Middle Cambrian age (Blaker, 1986, 1991; see also Higgins *et al.*, 1991), but all the collections described here are of Middle Cambrian age. Trilobites of only Middle Cambrian age have been previously reported from the Kap Stanton Formation (Fletcher *et al.*, 1988; Babcock & Robison, 1989; Robison & Babcock, 1990).

Locality 1 (Figs 1, 2), at Hand Bugt, Nyeboe Land, includes a 90 m thick succession of the upper Henson Gletscher Formation and lower Kap Stanton Formation. Seven collections were obtained by J. S. Peel and M. R. Blaker in 1985 (Fig. 2).

Locality 2 (Figs 1, 3) includes basal beds of the Kap Stanton Formation on the east side of Frankfield Bugt, Nyeboe Land. Two collections containing trilobites were made by A. K. Higgins in 1985 (Fig. 3). GGU 319789 was collected from talus, but GGU 319790 was collected in place. GGU 319789 is interpreted to be of local origin because separate slabs in the two collections contain parts and counterparts of the same trilobites (e.g., *Olenoides* cf. *convexus*, Fig. 14.2).

Locality 3 (Figs 1, 4) includes basal beds of the Kap Stanton Formation on a cape on the east side of J. P. Koch Fjord, north of the island of Primus, western Peary Land. Four collections were made at the locality, one by A. K. Higgins in 1984, and the others by J. S. Peel and M. R. Blaker in 1985 (Fig. 4). The locality is approximately 40 km north of the type locality of the Holm Dal Formation (Fig. 1; see Peel, 1988).

Depositional environments

Similarities in major lithofacies and biofacies patterns indicate that Greenland and much of North America were united in a single continent, Laurentia, during Cambrian time (e.g., Palmer, 1974). Thick and widespread carbonate deposits support palaeomagnetic evidence that the continent was located in tropical latitudes (e.g., Scotese *et al.*, 1979; Scotese, 1987; Scotese & McKerrow, 1990; see Babcock, 1994, fig. 2).

The depositional settings of the Henson Gletscher Formation in Nyeboe Land and the Kap Stanton Formation in Nyeboe Land and Peary Land are described more fully and interpreted in an accompanying paper (Ineson *et al.*, 1994). Both formations represent deposition in an open-marine, mainly low-energy environment below normal wave base. Sedimentation occurred seaward of an extensive carbonate platform that bordered the craton. In the northern outcrop belt, a carbonate-starved, outermost shelf-slope environment is inferred for most of the Henson Gletscher Formation, and a carbonate slope apron to carbonate-starved outermost shelf setting is inferred for the Kap Stanton Formation. Poor circulation may have resulted in oxygen-deficient bottom waters that inhibited sediment bioturbators. Thinly laminated carbonate and siliciclastic muds and silts accumulated mainly from suspension; thin beds of coarser sediment probably represent

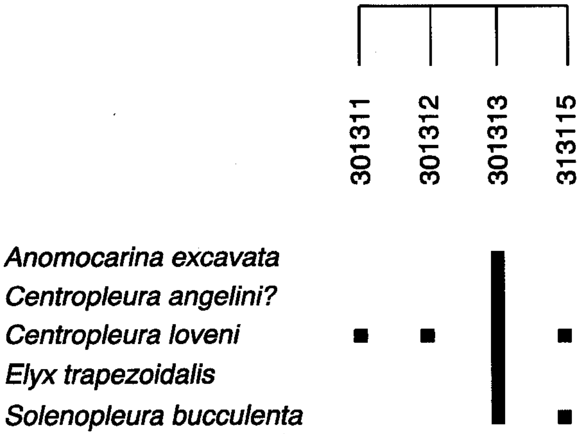


Fig. 4. Polymeroid trilobites in GGU collections from basal beds of the Kap Stanton Formation on a cape on the east side of J. P. Koch Fjord, north of the island of Primus, Peary Land (locality 3, Fig. 1). Collections are all from the lower part of the *Lejopyge laevigata* Interval-zone. GGU 301312, 301313, and 313115 are from the same stratigraphic level, and GGU 301311 is from approximately three metres lower in the section.


1


2

Fig. 5. Examples of major carbonate lithofacies from inferred deep-water environments, both × 1; polished slabs are cut perpendicular to bedding; 1, mudstone (MGUH 21.229) from GGU 313115, *Lejopyge laevigata* Zone; 2, packstone (MGUH 21.230) from GGU 319789, *Ptychagnostus atavus* Zone.

deposition from dilute turbidity currents or possibly storm-generated currents. Some intercalated grainstone or packstone beds represent episodic deposits resulting from tractional bottom currents.

Most trilobites in collections from the *Ptychagnostus gibbus* to *Lejopyge laevigata* zones are preserved in one of two carbonate lithofacies: packstone or mudstone (Fig. 5). Those from the *Glossopleura* zone, however, are in wackestone. More than 50 percent of the Henson Gletscher and Kap Stanton formations at locality 1 is dark grey to black limestone or dolostone. Most of the rock is lime mudstone with lesser amounts of argillaceous lime mudstone. Locally the mudstone grades to wackestone.

The mudstone facies (Fig. 5.1) is characterised by dark grey or black colour, thin bedding to millimetre-thick laminae, and lack of burrowing. Most bedding surfaces are planar and nearly parallel to slightly undulatory and discontinuous. The major constituent of the rock is fine-grained carbonate. Minor constituents are spar, clay- and silt-sized siliciclastics, and pyrite. Most of the fauna consists of agnostoid trilobites, polymeroid trilobites of Baltic aspect, and sponge spicules. Inarticulate brachiopods are rare. In mudstone, the presence of some articulated exoskeletons or molt assemblages and lack of obvious size sorting or fragmentation of disarticulated sclerites suggests that most of the trilobites lived at or near where their remains were deposited.

Packstone beds (Fig. 5.2) are of centimetre-scale thickness and are intercalated with mudstone. Locally they grade to grainstone or wackestone. Their bases truncate the mudstone laminae over which they were deposited. Where evident, grading is crude and fines upward. The tops of beds form sharp contacts with overlying millimetre-thick laminae of mudstone. In packstone, nearly all trilobites are disarticulated and the sclerites are commonly fragmented, crudely size sorted, and mixed with shells of hyoliths, hyolithellids, helcionelloids, inarticulate brachiopods, and ostracodes. Remains of trilobites of both Laurentian and Baltic aspect are present, although those of Laurentian aspect are much more common. Together, the evidence suggests that fossils in packstone beds were transported downslope as bioclastic debris by gravity flow. The total species diversity in packstone was probably increased by redeposition of bioclasts. Also, trilobites of slightly different ages may have been mixed, although evidence of such mixing was not detected. Foreign sediment was not found adhering to specimens, nor were clasts discovered in the packstones. Judging from the biostratigraphic ranges of taxa in the packstones, there is no association of polymeroids that cannot be attributed to ecological differences between biofacies.

Biostratigraphy

Both polymeroid and agnostoid trilobites are present in Middle Cambrian rocks of North Greenland although they do not always co-occur. They have very different stratigraphic and geographic distributions, which accords with inferred basic differences in their modes of life (e.g., Robison, 1976). Agnostoids, most of which were probably pelagic (Robison, 1972; Öpik, 1979), are found mainly in lithofacies representing open-shelf and slope environments. Polymeroids, most of which were benthic, are most abundant in open-shelf or restricted-shelf lithofacies. Separate biozones based on agnostoids and polymeroids have been proposed for some major Middle Cambrian biofacies (Robison, 1976). Zonation of polymeroids is described below, and the more refined zonation of agnostoids is discussed in an accompanying paper (Robison, 1994). In the systematic descriptions of taxa in this paper, reference is made to one or both sets of zonation, as appropriate.

The age of GGU collections 298971–298973 from near the middle of the Henson Gletscher Formation of locality 1 (Fig. 2) is based on only polymeroid trilobites because agnostoids are not present. All identified genera are relatively eurytopic and long-ranging and are widespread primarily in open-shelf lithofacies of Laurentia. The presence of *Glossopleura walcotti* in all three collections indicates that they belong to the *Glossopleura* Assemblage-zone of Robison (1976).

Trilobites representative of three of the four agnostoid interval-zones defined by Robison (1984) were found at locality 1. In ascending order these are the *Ptychagnostus gibbus*, *Ptychagnostus atavus*, and *Lejopyge laevigata* interval-zones. In North Greenland, taxa representing the *Ptychagnostus punctuosus* Zone were reported by Poulsen (1969; see also Robison, 1984, p. 35) from northern Nyeboe Land.

The *Ptychagnostus gibbus* Zone is represented by one collection, GGU 298970, from the Henson Gletscher Formation of locality 1 (Fig. 2). Although most polymeroids in the collection are long-ranging, the faunal association is consistent with a position close to the boundary between the *Oryctocephalus* and *Bolaspidella* assemblage-zones of Robison (1976).

The *Ptychagnostus atavus* Zone is represented by five collections. Three of them, GGU 298969, 298974, and 298975, are from the upper Henson Gletscher Formation of locality 1 (Fig. 2). GGU 298969 contains a species of *Syspacephalus* that may represent an upward extension in the observed range of this genus. Two other collections, GGU 319789 and 319790, are from basal beds of the Kap Stanton Formation of locality 2 (Fig. 3).

The *Lejopyge laevigata* Zone is represented by four collections, 301311 to 301313 and 313115, from the basal beds of the Kap Stanton Formation of locality 3 (Fig. 4). Of the identified polymeroids from North Greenland, all four genera and four of five species are also present in the informal lower *L. laevigata* Interval-zone of Robison (1984; equivalent to the zone of *Solenopleura brachymetopa* of Westergård, 1953), indicating a close correspondence in age with the Andrarum Limestone of Sweden (see Berg-Madsen, 1985).

Biogeography

As elaborated more fully in an accompanying paper (Babcock, 1994), Middle Cambrian rocks of the Henson Gletscher and Kap Stanton formations in Nyeboe Land and Peary Land contain polymeroid trilobites (which are described in this paper) of Laurentian and Baltic aspect. Polymeroids from the *Glossopleura* and *Ptychagnostus gibbus* zones are mostly of Laurentian aspect. Those in the *Ptychagnostus atavus* Zone are of mixed Laurentian and Baltic aspect, and those in the *Lejopyge laevigata* Zone are entirely of Baltic aspect.

Systematic descriptions

Terminology

Most morphological terms used here are defined in the *Treatise on Invertebrate Paleontology* (Harrington *et al.*, 1959a). Terms for lateral glabellar furrows and facial sutures are from Henningsmoen (1957, pp. 12–14). The term *genal bar*, applied to the family Paradoxididae, was defined by Öpik (1961). Morphological terms for genal caeca follow Jell (1978, pp. 251–253). The term *eye ridge* is used in a morphological sense even if part of the structure appears to belong to the caecal network. Terms for heterochronic processes follow McNamara (1986a, 1986b).

Repositories

All material referred to in this paper is identified by collection or museum numbers if known. Institutions and their acronyms are: Geological Survey of Greenland (Grønlands Geologiske Undersøgelse), Copenhagen (GGU); Geological Survey of Sweden, Uppsala (SGU); Geologisk Museum, Copenhagen (MGUH); Swedish Museum of Natural History (Naturhistoriska Riksmuseet), Stockholm (RM); Sedgwick Museum, Cambridge (SM); and U.S. National Museum of Natural History (Smithsonian Institution), Washington, D.C. (USNM).

Phylum Arthropoda
Class Trilobita

'Polymerida'

Remarks. The Polymerida has been treated by some authors as an order within the Trilobita. Based on phylogenetic analyses discussed under the 'Eodiscidae', the polymeroids are here interpreted to be a paraphyletic group defined as all trilobites exclusive of the highly derived Agnostida and the Nektaspida (see Fig. 27). The recent trilobite classification of Fortey (1990) cannot be applied at this time because of insufficient knowledge about ventral cephalic characters for many of the taxa discussed in

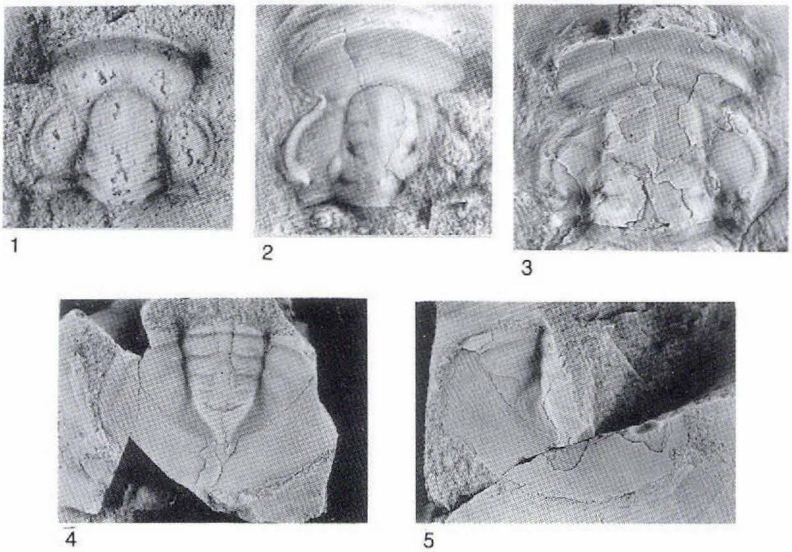


Fig. 6. *Anomocarina excavata* (Angelin). All specimens from GGU 301313.
1, small exfoliated cranidium, MGUH 21.231, × 8. 2, incomplete testaceous cranidium, MGUH 21.232, × 4. 3, incomplete, partly exfoliated cranidium, MGUH 21.233, × 2.5. 4, incomplete, partly exfoliated pygidium, MGUH 21.234, × 2. 5, incomplete, partly exfoliated pygidium, MGUH 21.235, × 2.

this paper. For convenience, therefore, the term polymeroid is used here, but only in an informal sense.

Family Anomocaridae Poulsen
Genus *Anomocarina* Lermontova, 1940

Anomocarina Lermontova, 1940, p. 156; Westergård, 1950, pp. 14, 17; Howell *in* Harrington *et al.*, 1959b, p. O287; Balashova *et al. in* Chernysheva, 1960, p. 92

Type species. *Proetus*? *excavatus* Angelin, 1851, p. 22.

Remarks. The generic concept of Westergård (1950, p. 14) is followed here.

Anomocarina excavata (Angelin, 1851)

Fig. 6

Proetus? *excavatus* Angelin, 1851, p. 22, pl. 18, fig. 3; Angelin, 1878, p. 22, pl. 18, fig. 3

Anomocare excavatum (Angelin). Angelin, 1854, p. 25; Angelin, 1878, p. 25, pl. 18, fig. 3; Brøgger (in part), 1878, pp. 39, 40, pl. 3, fig. 14a (not 14); Grönwall (in part), 1902, p. 140 (not pl. 4, fig. 6); Holm & Westergård, 1930, pp. 16, 17, pl. 2, figs 1–14, pl. 4, figs 19–21

Anomocarina excavatum (Angelin). Lermontova, 1940, p. 156, pl. 48, figs 3, 3a-m

Anomocarina excavata (Angelin). Westergård, 1950, pp. 17–19, pl. 3, figs 12–19; Kobayashi, 1962, pp. 107, 110, fig. 12b; Rosova, 1964, pp. 31, 32, pl. 1, figs 7–15, pl. 3, figs 21–23; Howell *in* Harrington *et al.*, 1959b, p. O287, fig. 212,*4*; Reyment, 1980, p. 8, figs 17a, 17b (copy of Angelin, 1878, pl. 18, fig. 3)

Anomocarina cf. *excavata* (Angelin). Westergård, 1950, p. 19, pl. 3, fig. 20

Lectotype. Pygidium, RM Ar. 1433.

New material. Two small- to medium-sized holaspid cranidia, two possible meraspid cranidia, and three holaspid pygidia; all in GGU 301313.

Remarks. The holaspides of *A. excavata* agree in all characters with specimens of similar size previously described or figured from Scandinavia (Westergård, 1950), Siberia (Lermontova, 1940), and Bennett Island (Holm & Westergård, 1930). Possible meraspid cranidia differ from larger specimens primarily in having somewhat narrower anterior areas of the fixigenae, a slightly longer preglabellar field, and slightly longer palpebral lobes.

Occurrence. Sclerites of *A. excavata* are present in dark mudstone of the basal beds of the Kap Stanton Formation at locality 3, Peary Land. Elsewhere, this species has been reported from Sweden, Norway, Denmark, Siberia, and Bennett Island. It has been reported from only the *Lejopyge laevigata* Interval-zone.

Family Conocoryphidae Angelin
Genus *Dasometopus* Resser, 1936

Dasometopus Resser, 1936, p. 22; Westergård, 1950, pp. 34, 35; Chernysheva, 1953, p. 16; Poulsen *in* Harrington *et al.*, 1959b, pp. O242, O243; Suvorova *in* Chernysheva, 1960, p. 117

Type species. *Harpides breviceps* Angelin, 1854, p. 87, by original designation (Resser, 1936, p. 22).

Emended diagnosis. Cephalon semicircular, much wider than long; anterior margin broadly rounded, rarely straight medially; border narrow, may be thickened. Glabella subconical, approximately half cranidial length, widest at base, tapering forward; with three distinct pairs of lateral furrows. Preglabellar field having longitudinal depression. Gena moderately convex, covered with inosculating type 4 caeca. Facial suture absent. Caecal ridge of type 3, distinct. Eyes absent. Thorax with about 24 segments; axis narrow; pleura more than twice as wide as axis, flattened, with distinct interpleural furrow, terminating in long, narrow, backwardly directed spine, marginal spine on twelfth segment greatly elongated, width of pleural lobe decreasing backward from twelfth segment. Pygidium micropygous, subtriangular, having short, narrow marginal spines.

Remarks. Representatives of *Dasometopus* are presently known from Sweden, Denmark, Siberia, and North Greenland. Described species include *D. breviceps* (Angelin, 1854), *D. latus* Korobov, 1973, *D. granulatus* Korobov, 1973, *D. maensis* Korobov, 1973, *D. munacaensis* Korobov, 1973, *D. rectus* Korobov, 1973, and *D. groenlandicus* n. sp. Another species, *D.? incertus* Westergård, 1950, from Sweden, may represent an undescribed genus. It is discussed further in remarks on *Elyx*.

Specimens of *Dasometopus* from Sweden are in the *Ptychagnostus punctuosus* and *Lejopyge laevigata* interval-zones. Those from Siberia range from the *Paradoxides hicksii – Tomagnostus fissus* Zone through the *Anomocarioides limbataeformis* Zone of Korobov (1973), which probably corresponds to a range from the *Ptychagnostus atavus* through *Lejopyge laevigata* zones of Robison (1984). New specimens from North Greenland are in the *P. atavus* Zone.

Dasometopus groenlandicus n. sp.

Fig. 7

Etymology. From Grønland (Greenland).

Holotype. Cephalon, MGUH 21.236.

Material. One small complete cephalon and numerous fragments of larger cephala in GGU 319789 and 319790.

Diagnosis. *Dasometopus* having posterior cephalic margin slightly bowed forward over most of its length; border thickened anteriorly and laterally; border furrow moderately wide medially, narrowing slightly at sides; glabella tapering very slightly toward anterior, bluntly rounded anteriorly; large baccula present in axial furrow; eye ridge strong, arcuate, extending nearly to border; surface covered with widely spaced granules except on axis and border.

Description. Cephalon nearly twice as wide as long, evenly rounded through anterior and lateral margin, posterior margin slightly bowed forward over most of length; border narrow, thickened anteriorly and laterally, upturned posteriorly; border furrow shallow, moderately wide medially, narrowing slightly laterally; posterior border furrow deep, moderately wide. Glabella convex, raised above gena; slightly less than one-half cranidial length; widest at L1, slightly tapering forward; bluntly rounded anteriorly; lateral furrows distinct, deep at back,

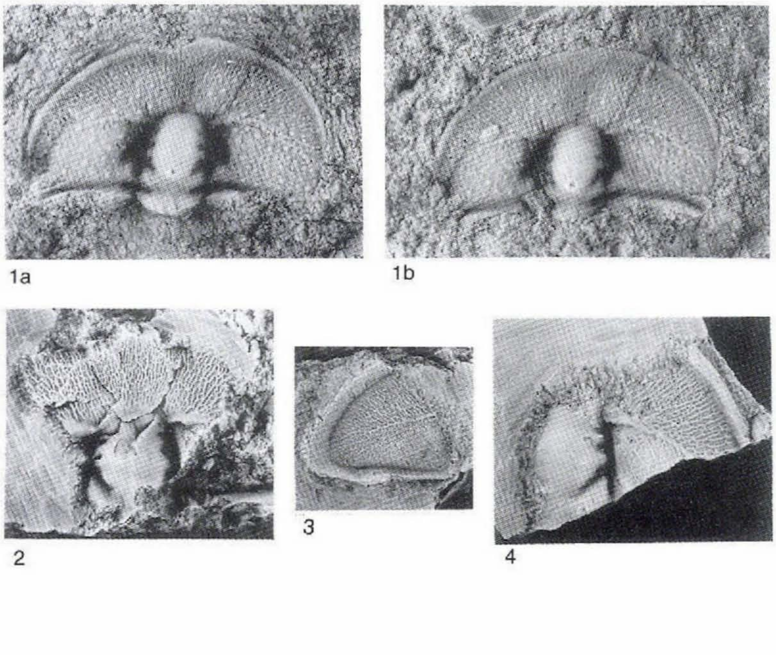


Fig. 7. *Dasometopus groenlandicus* n. sp. All specimens from GGU 319790.
1, holotype cephalon (a) and latex cast of counterpart (b), MGUH 21.236, × 10. 2, incomplete cephalon, MGUH 21.237, × 2.5. 3, incomplete cephalon, MGUH 21.238, × 2.5. 4, incomplete cephalon, MGUH 21.239, × 2.5.

slightly shallowing forward; S1 bifurcate, oblique backwards; S2 and S3 transverse. Occipital ring convex, without node or spine; occipital furrow moderately wide and shallow medially, deep and narrow at side. Gena moderately convex, comprising large raised area behind caecal ridge and smaller raised area in front of caecal ridge, separated by wide, shallow depression; covered with inosculating caeca, some connecting with caecal ridge; raised lines stronger in front of caecal ridge. Preglabellar field wide, subequal in length with glabella; preglabellar depression wide, shallow. Axial furrow distinct, wide posteriorly, narrowing anteriorly; baccula present in posterior one-quarter. Caecal ridge strong, arcuate; beginning in axial furrow at middle of L4, extending nearly to border. Facial suture and eye absent. Surface of genae covered with strong, widely spaced granules.

Thorax and pygidium unknown.

Remarks. Cephala of *D. groenlandicus* n. sp. differ from those of all other species in the genus by the combination of a posterior border that is slightly bowed anteriorly over most of its length, a glabella that slightly tapers forward and is bluntly rounded anteriorly, the presence of bacculae in the axial furrows, and the presence of widely spaced granules on the genae.

The holotype cephalon of *D. groenlandicus* is small for the species and is probably a young holaspid. Although it is only one-sixth the maximum observed cranidial length, it does not seem to differ significantly in proportion or surface markings from larger specimens.

Occurrence. Broken cephala are relatively common in dark mudstone beds of the basal Kap Stanton Formation at locality 2, Nyeboe Land. They are associated with trilobites indicative of the *Ptychagnostus atavus* Interval-zone.

Genus *Elyx* Angelin, 1851

Eryx Angelin, 1851, p. 4 [corrected to *Elyx*, 1854, p. X]; Lindström, 1901, p. 10

Elyx Angelin, 1854, p. X; Angelin, 1878, p. 4 [incorrectly cited as *Eryx*; corrected p. X]; Howell, 1937, p. 1169; Westergård, 1950, p. 32; Poulsen *in* Harrington *et al.*, 1959b, pp. O243, O244; Lermontova *in* Chernysheva, 1960, p. 118; Hutchinson, 1962, p. 98

Type species. Eryx laticeps Angelin, 1851, p. 4, by monotypy.

Emended diagnosis. Cephalon truncated anteriorly, much wider than long; anterior margin very slightly rounded, straight, or concave medially; anterolateral margin angular to very narrowly rounded; posterolateral margin rounded; border narrow, convex, upturned anteriorly; border furrow deep; preglabellar boss joins anterior border. Glabella subconical, convex, widest at base, moderately tapering forward, truncated anteriorly, with 3 pairs of lateral furrows. Gena convex. Facial suture and eyes absent.

Thorax with 11 to 13 segments. Axis narrow, convex. Pleurae wide, flattened, tips falcate; pleural furrows shallow, wide.

Pygidium small.

Remarks. Eryx was erected by Angelin (1851, p. 4) but, in a corrigendum published in the second fasciculus of the same work (1854, p. X), the name was emended to *Elyx*. The change in spelling is demonstrably intentional (see *International Code of Zoological Nomenclature*, Art. 33 (b) (i); International Commission on Zoological Nomenclature, 1985), and the spelling *Elyx* has been subsequently adopted by all authors except Lindström (1901). Westergård (1950, p. 32) stated that the name of this trilobite was emended because *Eryx* was preoccupied, but Angelin did not state a reason for the emendation. The date of publication of *Elyx* is 1851, the year in which the misspelled name was first used.

Nine described species, all of middle to late Middle Cambrian age, are here included in *Elyx*: *E. laticeps* (Angelin, 1851) from Sweden, Denmark, Norway, and Siberia; *E. matthewi* Hutchinson, 1962, from south-eastern Newfoundland; *E. trapezoidalis* n. sp. from North Greenland; and *E. alatus* Korobov, 1973, *E. arcus* Korobov, 1973, *E. graevis* Korobov, 1973, *E. nelegerensis* Korobov, 1973, *E. olenekensis* Korobov, 1973, and *E. palmeri* Korobov, 1973, all from Siberia. Another species, *E. americanus* Howell, 1932, from St. Albans, Vermont, was transferred to *Ctenocephalus* (Resser, 1936, p. 20). *E. latilimbatus* Brøgger, 1878, is known from a single cephalon that was only illustrated by a drawing (Brøgger, 1878, pl. 3, fig. 10). The specimen is probably an external mould of a conocoryphid trilobite but not *Elyx*. Although the anterior margin is concave medially, the figure shows no evidence of angular or narrowly rounded anterolateral corners or a preglabellar boss. The slightly tapering glabellar sides, wide anterior border, and wide lateral border are also different from those of *Elyx*.

Two conocoryphid species assigned by Korobov (1973) to *Elyx*, *E. shatskii* Korobov, 1973, and *Dasometopus*? *incertus* Westergård, 1950, are of questionable affinity and possibly represent an undescribed genus. *D.*? *incertus* was based on a single fragmentary cephalon from the Andrarum Limestone of Scania, Sweden. *E. shatskii* was illustrated by two cephala from the *Anomocarioides limbataeformis* Zone of Siberia (Korobov, 1973). Some important cephalic characters that distinguish these two species from *Elyx* are a semicircular outline without angular or narrowly rounded anterolateral corners, a glabella that is approximately half the length of the cranidium, and the presence of a narrow medial ridge in the preglabellar field rather than a subcircular boss. They differ from *Dasometopus* primarily in having a medial preglabellar ridge rather than a furrow, and a distinct border furrow.

Some authors (Grönwall, 1902; Strand, 1929; Resser, 1936, 1937a) have regarded *Elyx* to be a junior synonym of *Ctenocephalus* Corda, 1847, but I agree with Howell (1937), Westergård (1950), Poulsen *in* Harrington *et al.* (1959b), and Hutchinson (1962) in recognising that characters of the cephalon are sufficient to distinguish the two genera. In addition to differential characters listed by Westergård (1950, p. 32), *Elyx* differs from *Ctenocephalus* in the apparent lack of facial sutures. Westergård (1950, p. 32) stated that facial sutures, if developed, are marginal, but a specimen of *Elyx* showing sutures has not been reported. Specimens of *E. trapezoidalis* n. sp. from North Greenland, which are preserved in relief, show that facial sutures are not present dorsally, marginally, or ventrally.

One species, *E. matthewi*, was described (Hutchinson, 1962, p. 99) as having well-rounded anterolateral corners, not angular, as are usual for the genus. Of the four specimens identified by Hutchinson (1962, pl. 13, figs 3–6) as *E. matthewi*, however, none shows an intact anterolateral margin. A small cephalon of a conocoryphid trilobite that was figured by Hutchinson (1962, pl. 12, fig. 16) as *Ctenocephalus* (*Hartella*) *terranovicus* Resser, 1925, agrees in all characters with *Elyx* and differs from *Ctenocephalus*. That specimen, which probably belongs to *E. matthewi*, has a nearly complete, and evidently angular, anterolateral corner.

Specimens of *Elyx* from Sweden and Norway are in the *Lejopyge laevigata* Interval-zone. Those from Siberia range from the *Corynexochus perforatus* – *Anopolenus henrici* Zone through the *Anomocarioides limbataeformis* Zone of Korobov (1973), which probably corresponds to a range from the *Ptychagnostus atavus* through *Lejopyge laevigata* zones of Robison (1984). New specimens from North Greenland are in rocks of the *L. laevigata* Zone.

Elyx trapezoidalis n. sp.

Fig. 8

Etymology. From Latin, *trapezoides*, referring to the trapezoidal outline of the cephalon.

Holotype. Cephalon, MGUH 21.240.

Material. Eight cephala or fragmentary cephala in GGU 301313.

Diagnosis. *Elyx* having comparatively short cephalon with subtly angular anterolateral corner, lateral border almost straight, genal angle broadly rounded, gena most convex on line with preglabellar furrow.

Description. Cephalon trapezoidal, short (sag.) for genus, anterior border slightly concave medially, anterolateral corners subtly angular, lateral border nearly straight and slightly converging forward, posterolateral corners broadly rounded. Axial furrows deep. Glabella elevated well above gena; S1 and S2 short, deep at side, oblique backward; S3 reduced to shallow pit. Occipital furrow deep at side, shallow medially. Occipital ring broken on all specimens, may have node or spine. Preglabellar field consisting of strong, well-defined boss. Gena convex, highest on line with preglabellar furrow, steeply sloping at margin to anterior and lateral section of border furrow and slightly sloping backward to posterior section of border furrow. Caecal ridge of type 3, weak, short, beginning forward of S1 and directed obliquely backward then laterally. Facial suture lacking. Surface of test covered with fine, closely spaced granules and larger, irregularly spaced granules, except in furrows; larger granules also present on internal mould.

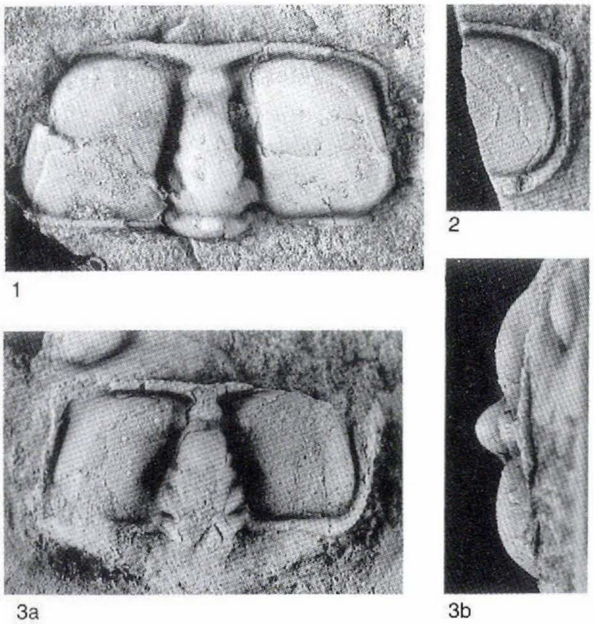


Fig. 8. *Elyx trapezoidalis* n. sp. All specimens from GGU 301313.

1, latex cast of holotype cephalon, MGUH 21.240, × 2. 2, right side of small cephalon MGUH 21.241, × 6. 3, mostly exfoliated cephalon in dorsal (a) and frontal (b) views, MGUH 21.242, × 4.

Thorax and pygidium unknown.

Remarks. The cephalon of *Elyx trapezoidalis* n. sp. differs in outline and minor surface characters from that of other species of the genus. In having a comparatively short cephalon, which is concave along its anteromedial margin, *E. trapezoidalis* most closely resembles *E. laticeps* (Angelin, 1851) and *E. matthewi* Hutchinson, 1962. The anterolateral corners of *E. trapezoidalis*, however, are less angular than those of *E. laticeps*. At the anterolateral corner, the anterior border is lower than the lateral border of *E. matthewi* but not of *E. laticeps*. *E. trapezoidalis* has less well defined caecal ridges and S3 furrows than either *E. laticeps* or *E. matthewi*. Finally, the lateral margins of *E. trapezoidalis* are straighter than those of either *E. laticeps* or *E. matthewi*.

Occurrence. E. trapezoidalis is present in dark lime mudstone beds of the basal Kap Stanton Formation at locality 3, Peary Land.

Genus *Hartshillia* Illing, 1916

Hartshillia Illing, 1916, p. 424; Lake, 1938, pp. 262, 263, 268; Vodges, 1925, p. 101; Poulsen *in* Harrington *et al.*, 1959b, p. 0244; Hutchinson, 1962, p. 109

Type species. Holocephalina inflata Hicks, 1872, p. 178, by subsequent designation (Vogdes, 1925, p. 101).

Emended diagnosis. Cephalon semicircular, strongly convex, lacking border; external furrows mostly to completely effaced, but axial and S1 furrows well-defined on internal surface, other lateral glabellar furrows rarely expressed on internal surface. Glabella long, narrowest posteriorly, expanding forward; maximum width 0.3 to 0.5 times maximum cephalic width. Occipital ring with strong medial spine. Frontal area short. Fixigena strongly convex. Genal angle rounded, angular, or with genal spine. Facial suture probably absent. Eyes absent. Posterior border furrow weak, margin concave.

Labrum ovoid, central body convex, anterior wings large, border moderately wide.

Thorax with at least 8 segments. Axis slightly narrower than pleural lobe, convex. Pleural lobe nearly flat. Pleural groove straight for most of length, turned backward near pleural tips. Pleural tips short, falcate.

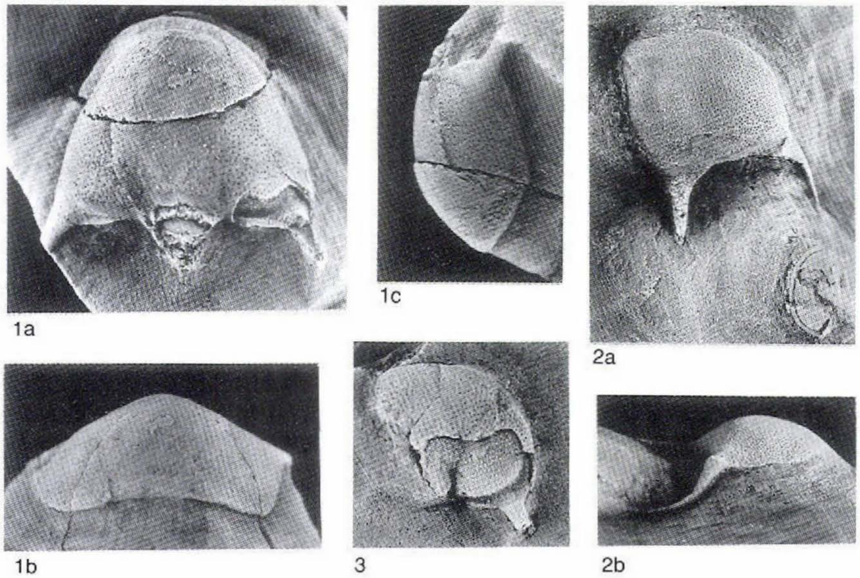
Pygidium small. Axis about as wide as pleural lobe, with 2 to 5 rings. Border wide, downwardly sloping.

Remarks. Hartshillia presently includes five species: *H. inflata* (Hicks, 1872), *H. terranovica* Hutchinson, 1962, *H. clivosa* Lazarenko, 1965, *H. pusilla* Lazarenko, 1965, and *H. taimyrica* Lazarenko, 1965. Two species originally assigned to *Hartshillia* have been transferred to other genera. *H. spinata* Illing, 1916, was reassigned as the type species of the conocoryphid *Hartshillina* Lake (1940, p. 300), and *H. marocana* Gigout, 1951, was reassigned as the type species of the ellipsocephalid *Mesetaia* Hupé (1953, p. 158). Illustrated specimens from Morocco (Termier & Termier, 1950, pl. 191, figs 22–27) were misidentified as *Hartschillia* [*sic*] sp. Although the line drawings are poor, they are adequate to show that the specimens are not effaced, and have facial sutures and eyes. Although identification of the Moroccan specimens is uncertain, they resemble a generalised ptychopariid.

Marginal facial sutures have been reported in only *H. inflata*, the type species, but their presence is questionable. Illing (1916, p. 424) stated that "most of the specimens have no free cheeks, but some forms show a narrow border broken away from the head which appears to correspond to the free cheek, and it would appear probable that the facial suture was almost marginal and continuous in front." Later, Lake (1938, p. 268) reported that no facial sutures are shown on the upper surface, and Poulsen (*in* Harrington *et al.*, 1959b, p. 0244) reported that facial sutures were "apparently marginal." Facial sutures, if present in this species, are not convincingly illustrated in any of Illing's figures, nor are they present in any of the well-preserved specimens of *H. inflata* from North Greenland. Illing's figured specimens are preserved in shale and are crushed. They are predominantly internal moulds, but the margins of the now-missing test are defined by external moulds. Illing may have been misled by some artifact of preservation, and his material should be re-examined for the presence of facial sutures.

Where present in well-dated rocks, *Hartshillia* appears to be restricted to the middle and upper Middle Cambrian. *Hartshillia inflata* has been identified from St. Davids, Wales, and near Nuneaton, England, where it occurs with trilobites indicative of the *Ptychagnostus atavus* and *P. punctuosus* interval-zones. Specimens apparently belonging to *H. inflata* are associated with fossils of the *P. atavus* Zone in North Greenland. In southeastern Newfoundland, *H. terranovicus* is associated with trilobites indicative of the *P. atavus* Zone. Specimens described from Siberia (Lazarenko, 1965) are from the *Paradoxides hicksii – Tomagnostus fissus* and *Corynexochus perforatus – Anopolenus henrici* zones of Korobov (1973), and probably correspond in age to the *Ptychagnostus gibbus* through *P. atavus* zones of Robison (1984).

Fig. 9. *Hartshillia inflata* (Hicks). All specimens from GGU 298969. 1, cephalon in dorsal (a), frontal (b), and left-lateral (c) views, MGUH 21.243, × 5. 2, incomplete cranidium in dorsal (a) and right-lateral (b) views, MGUH 21.244, × 5. The right genal spine was broken and healed during life. Cephalon of *Eodiscus scanicus* (Linnarsson) to lower right of photograph (MGUH 21.245). 3, partly exfoliated cephalon, MGUH 21.246, × 6.



Hartshillia inflata (Hicks, 1872)

Fig. 9

Holocephalina inflata Hicks, 1872, p. 178, pl. 6, figs 8–10; Reed, 1898, p. 497; Grönwall, 1902, p. 87

Hartshillia inflata (Hicks). Illing, 1916, pp. 424, 425, pl. 34, figs 1–5; Vogdes, 1925, p. 101; Lake, 1938, p. 268, pl. 38, figs 6–15; Lake, 1940, p. 300; Poulsen *in* Harrington *et al.*, 1959b, p. O244, fig. 181,9; Morris, 1988, p. 106

Lectotype. Incomplete thorax and attached pygidium, SM A469, selected by Morris (1988, p. 106).

New material. Four cephala in GGU 298969.

Remarks. *Hartshillia* is represented by four cephala that seem to fall within the range of variation of specimens of *H. inflata* illustrated by Hicks (1872), Illing (1916), and Lake (1938) from England.

The new cephala range from semicircular to anteriorly elongate in outline, and have a width approximately 1.5 times the length. The single uncrushed specimen (Fig. 9.1) is very convex and has a strongly arched anterior border. Some of the variation in outline and convexity among specimens in the sample is evidently due to crushing. In the most extreme example (Fig. 9.3), evidence of the anterior arch is absent. All specimens are completely effaced, and covered with fine, densely spaced puncta. Furrows are not expressed on the outer surface but their positions are indicated by narrow linear bands lacking puncta. The position of the axial furrow is only indicated posteriorly. The genal spines are moderately long, narrow, straight, and impunctate. They extend backward from the posterior margin and, in profile view, are approximately three-fifths of the way up from the ventral edge of the cephalon. The occipital spine is short and strong. Facial sutures are absent.

Two partially exfoliated specimens reveal furrows and fine, closely spaced granules on the internal mould. The axial furrow is well defined posteriorly, and diverging and shallowing anteriorly. Both the occipital furrow and the posterior border furrow are well defined. The exoskeleton is thick over the effaced furrows and moderately thick elsewhere.

One specimen (Fig. 9.2) has a broken and healed right genal spine. The means by which breakage occurred is considered to be uncertain (see Babcock, 1993). The spine was broken near its base as indicated by an irregularly swollen knob. Where regrown, the spine is not straight as is usual, but is strongly curved downward and backward. In life, it evidently projected below the lower edge of the cranidium, suggesting that this species was pelagic, rather than benthic.

Previously, the cranidium of *H. inflata* has been described as having a punctate (Hicks, 1872, p. 178) or finely granulate (Illing, 1916, p. 424; Lake, 1938, p. 269) surface. The new material indicates that the external surface of the test is punctate and the internal mould is granulate.

Termier & Termier (1950, p. 29, pl. 185, fig. 25) reported *H. inflata* from Morocco, but the cranidium upon which their determination was made was misidentified. The specimen, illustrated by only a line drawing, is twice as wide as long exclusive of the occipital spine, has facial sutures, and appears to be completely effaced ex-

Fig. 10. *Corynexochus*? sp.; broken and crushed cranidium, MGUH 21.247 from GGU 319790, × 10.

cept for the anterior and posterior border furrows. The specimen cannot be identified to genus from the original illustration, but the great relative width, the presence of facial sutures, and the presence of an anterior border furrow demonstrate that it is not *Hartshillia*.

Occurrence. *H. inflata* is present in wackestone 71 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. It is associated with trilobites of the *Ptychagnostus atavus* Zone. The species has been previously reported from various localities in the English Midlands (Hicks, 1872; Illing, 1916; Lake, 1938), where it occurs with trilobites indicative of the *Ptychagnostus atavus* and *P. punctuosus* interval-zones.

Family Corynexochidae Angelin
Genus *Corynexochus*

Corynexochus? sp.
Fig. 10

Remarks. A species of corynexochid, probably *Corynexochus*, is represented by a single, small, fragmentary, crushed cranidium in GGU 319790. The cranidium is characterised by a glabella that reaches to the anterior border and that is strongly expanded anteriorly. Three weak lateral glabellar furrows are present; S1 is directed obliquely backward; S2 and S3 seem to be shallow depressions at the axial furrow. The anterior area of the fixigena is narrow, and approximately one-third as wide as the posterior area. The palpebral lobes are moderately long.

Occurrence. Present in the basal beds of the Kap Stanton Formation at locality 2, Nyeboe Land. It occurs with trilobites indicative of the *Ptychagnostus atavus* Interval-zone.

Family Dolichometopidae Walcott
Genus *Bathyuriscus* Meek, 1873

Bathyuriscus Meek, 1873, p. 484; Walcott, 1886, p. 215; Walcott, 1916, pp. 330–334; Resser, 1935, p. 13; Kobayashi, 1942a, p. 155; Kobayashi, 1942b, p. 471; Lake, 1934, p. 186; Shimer & Shrock, 1944, p. 607; Poulsen *in* Harrington *et al.*, 1959b, p. O224; Robison, 1964, p. 534; Palmer, 1968, p. B44; Robison, 1976, p. 102; Young & Ludvigsen, 1989, pp. 14, 15

Orria Walcott, 1916, p. 379; Kobayashi, 1942a, p. 172; Kobayashi, 1942b, p. 473; Shimer & Shrock, 1944, p. 613; Poulsen *in* Harrington *et al.*, 1959b, p. O224

Oriella Rasetti, 1948b, p. 329; Poulsen *in* Harrington *et al.*, 1959b, p. O225

Wenkchemnia Rasetti, 1951, pp. 183, 184; Poulsen *in* Harrington *et al.*, 1959b, p. O226; Suvorova & Chernysheva *in* Chernysheva, 1960, p. 76

Type species. *Bathyurus*(?) *haydeni* Meek, 1873, p. 484, by original designation (Meek, 1873, p. 484).

Remarks. The generic diagnosis of Robison (1964, pp. 534, 535) is followed here. It is modified, however, to cite only one pair of fossulae, rather than two pairs, in the axial furrow. Based on examination of a large number of specimens in the U.S. National Museum and at the University of Kansas, I agree with the conclusion that *Wenkchemnia* is a junior synonym of *Bathyuriscus* (Robison, 1976, p. 102), although detailed evidence supporting that conclusion has yet to be published.

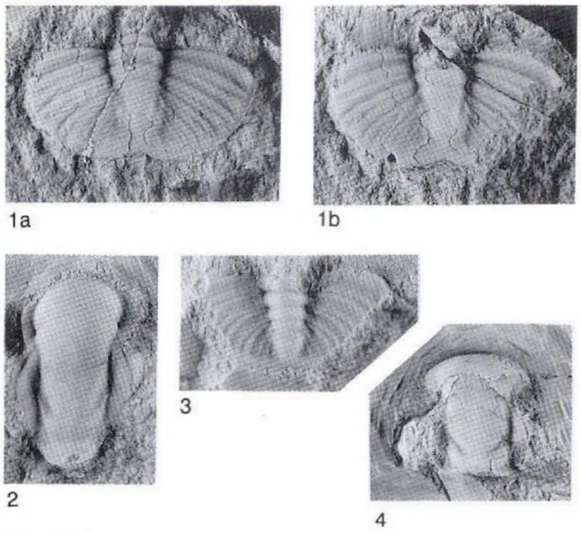


Fig. 11. Specimens of *Bathyuriscus*.

1–2, *Bathyuriscus concavus* n. sp., both from GGU 319790. 1, holotype pygidium (a) and latex cast of counterpart (b), MGUH 21.248, × 3. 2, incomplete cranidium, MGUH 21.249, × 2.

3–4, *Bathyuriscus* sp., both from GGU 298970. 3, incomplete pygidium, MGUH 21.250, × 5. 4, incomplete cranidium, MGUH 21.251, × 2.

Bathyuriscus concavus n. sp.

Fig. 11.1, 2

Etymology. From Latin, *concavus*, hollowed or arched inward, referring to the posteromedial notch in the pygidium.

Holotype. Pygidium, MGUH 21.248.

Material. One cranidium and two pygidia in GGU 319790.

Diagnosis. Cranidium having fixigena with narrow anterior area. Lateral glabellar furrows weak; axial furrow moderately shallow; fossula moderately deep. Pygidium with distinct posteromedial notch; axis with four rings and long terminal piece; pleural lobe with six pleural furrows and five interpleural furrows.

Description. Cranidium known from only one broken specimen. Glabella moderately convex, long, slender posteriorly, expanding evenly forward, extending nearly to anterior margin; lateral furrows weak. Axial furrow moderately shallow, fossula moderately deep. Occipital ring broken medially, but evidently with node or spine. Fixigena wide anteriorly, relatively narrow just behind palpebral lobe, posterior area not preserved. Palpebral lobe gently curved, moderately well-defined by weak palpebral furrow; length about one-half of glabellar length; anterior end of palpebral furrow intersects axial furrow just behind fossula. Posterior border not preserved. Librigena unknown. Surface smooth.

Thorax unknown.

Pygidium transverse, width about twice length, having distinct posteromedial notch, anterolateral spine absent. Axis low, moderately tapering, anterior width more than one-quarter width of pygidium; having 4 rings, long terminal piece, and postaxial ridge extending almost to posterior border. Axial furrows shallowing posteriorly. Pleural field low, with 6 moderately wide pleural furrows and 5 narrower interpleural furrows. Surface smooth.

Remarks. B. concavus differs from all other species of the genus in having a moderately short and wide pygidium with four rings and a long terminal piece in the axis, six pleural furrows, and a distinct posteromedial notch.

Two species from Utah, *B. brighamensis* Resser, 1939a, and *B. wasatchensis* (Resser, 1939b), also have distinct posteromedial notches in the pygidium. The pygidium of *B. concavus* is slightly narrower and less triangular in outline than that of *B. brighamensis.* It also differs in the lack of small anterolateral spines, which are present in some specimens of *B. brighamensis. B. concavus* differs from *B. wasatchensis* in having a more transverse outline, and lacking well-developed anterolateral spines.

Occurrence. Rare in packstone of the basal beds of the Kap Stanton Formation at locality 2, Nyeboe Land. It is associated with trilobites indicative of the *Ptychagnostus atavus* Interval-zone of Robison (1984).

Bathyuriscus sp.

Fig. 11.3, 4

Material. Two cranidia and two pygidia in GGU 298970.

Remarks. Four sclerites belonging to this unassigned species are in GGU 298970. They are from small holaspides and are too poorly preserved for meaningful comparison with other species.

The available cranidia are fragmentary. The glabella is moderately long for the genus and wide anteriorly. Only the S1 and S2 furrows are distinct, the S1 furrows being moderately deep. The fossulae are moderately deep. The anterior area of the fixigena is narrow. The palpebral lobes are incomplete.

The available pygidia are small and broken. They appear to have been relatively transverse, and without a distinct posteromedial notch. The axis is relatively convex, moderately tapering, and contains five rings, a terminal piece, and a postaxial ridge. The pleural field is low, and has five wide pleural furrows and four narrower interpleural furrows. The surface is smooth.

Occurrence. Rare in a packstone bed from approximately 56 m above the base of the Henson Gletscher Formation at locality 1. It is associated with trilobites indicative of the *Ptychagnostus gibbus* Interval-zone of Robison (1984).

Genus *Glossopleura* Poulsen, 1927

Glossopleura Poulsen, 1927, p. 268; Kobayashi, 1935, p. 132; Shimer & Shrock, 1944, p. 611; Rasetti, 1951, p. 163; Palmer, 1954, p. 67; Rusconi, 1954; Poulsen *in* Harrington, 1959b, p. O224; Suvorova & Pokrovskaia *in* Chernysheva, 1960, p. 76; Poulsen, 1964, p. 25

Bathyuriscus (*Glossopleura*) Poulsen. Kobayashi, 1942a, pp. 159, 160; Kobayashi, 1942b, p. 471 [misspelled *Glossopheura*]

Sonoraspis Stoyanow *in* Cooper *et al.*, 1952, pp. 50–53

Type species. Dolichometopus boccar Walcott, 1916, p. 363; by original designation (Poulsen, 1927, p. 268).

Remarks. The generic concept of Palmer (1954, p. 67) is followed here. His diagnosis is emended, however, to include species having a short anterior border in front of the glabella, a small node on the occipital ring, or medial nodes or spines on the axial lobe of some thoracic segments.

More than 50 species of *Glossopleura* have been described from western North America, North Greenland, and the Precordillera terrane of Argentina. Many species are in need of re-evaluation, but discriminating among some species can be difficult because furrows on the dorsal surface are generally weakly expressed in holaspides and because exoskeletal convexity, which has been used as a character for diagnosing species, can be influenced by compaction. The pygidial outline and width of the pygidial border can vary within rather wide limits in a species, as shown by specimens of *G. walcotti* (Fig. 12.3–12.6).

Glossopleura walcotti Poulsen, 1927

Figs 12; 13.6

Glossopleura walcotti Poulsen, 1927, pp. 268, 269, pl. 16, figs 20–30; Poulsen, 1946, p. 318; Poulsen, 1964, pp. 25–29, pl. 1, figs 2–4, text-figs 3, 4; Palmer & Halley, 1979, p. 79, pl. 16, figs 6–8, 11–19

Glossopleura expansa Poulsen (in part), 1927, p. 269, pl. 16, fig. 32

Glossopleura longifrons Poulsen (in part), 1927, p. 272, pl. 17, fig. 10

Lectotype. Cranidium, MGUH 2277, designated by Poulsen (1964, p. 26).

New material. Twenty-five sclerites in GGU 298971–298973.

Remarks. Sclerites of *G. walcotti* are common in several sections in North Greenland. Morphological variation in this species has been discussed by Poulsen (1964, pp. 25–27), who also reassigned specimens previously referred to other species. New specimens of *Glossopleura* from Nyeboe Land all fall within the limits of variation of *G. walcotti* as outlined by Poulsen (1964).

Occurrence. *G. walcotti* is widespread in open-shelf lithofacies of the *Glossopleura* Assemblage-zone in North Greenland and the western United States. New material is from wackestone approximately 42 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. The species has been previously reported from the Cape Wood Formation of North-West Greenland (Poulsen, 1927; Poulsen, 1964) and the Carrara Formation of Nevada and California (Palmer & Halley, 1979).

Family Dorypygidae Kobayashi

Genus *Kootenia* Walcott, 1889

Bathyuriscus (Kootenia) Walcott, 1889, p. 446

Kootenia Walcott. Walcott, 1918, p. 131; Walcott, 1925, p. 92; Kobayashi, 1935, pp. 156, 192; Resser, 1937b, p. 15; Resser, 1938, p. 84; Deiss, 1939, p. 100; Resser, 1939a, p. 15; Resser, 1939b, p. 46; Lermontova, 1940, p. 139; Resser, 1942, p. 27; Howell, 1943, p. 244; Shimer & Shrock, 1944, p. 613; Resser, 1945, p. 199; Rasetti, 1948a, p. 14; Rasetti, 1948b, p. 332; Thorslund, 1949, p. 4; Lermontova, 1951, p. 122; Rasetti, 1951, p. 188; Lochman *in* Cooper *et al.*, 1952, p. 121; Hupé, 1955, p. 9; Palmer, 1954, p. 64; Ivshin, 1953, p. 37; Lochman, 1956, p. 1390; Poulsen *in* Harrington *et al.*, 1959b, p. O218; Suvorova & Pokrovskaia *in* Chernysheva, 1960, p. 78; Lermontova, 1951, pp. 122–124; Chernysheva, 1961, p. 126; Lazarenko, 1962, p. 60; Termier & Termier, 1950, pl. 187, figs 3, 4; Suvorova, 1964, pp. 86–90; Demokidov & Lazarenko, 1964, p. 2041; Egorova *et al.*, 1960, p. 192; Fritz, 1972, p. 35; Young & Ludvigsen, 1989, p. 17

Dorypyge Matthew, 1899, p. 56

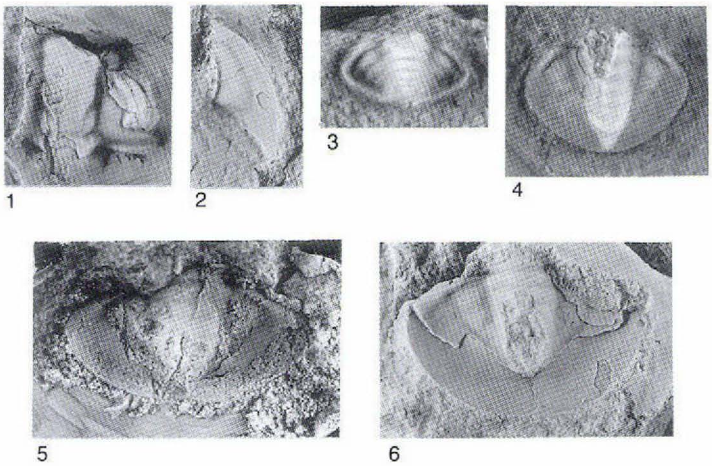


Fig. 12. *Glossopleura walcotti* Poulsen. All specimens from GGU 298971, unless otherwise stated. 1, incomplete cranidium, MGUH 21.252, × 2.5. 2, librigena, MGUH 21.253, × 3. 3, smallest observed pygidium, MGUH 21.254, × 16. 4, small pygidium, MGUH 21.255, × 8. 5, pygidium, MGUH 21.256 from GGU 298972, × 3. 6, pygidium, partly exfoliated, MGUH 21.257, × 2.5.

Notasaphus Gregory, 1903, p. 155; Whitehouse, 1939, pp. 241–243

Type species. Bathyuriscus (*Kootenia*) *dawsoni* Walcott, 1889, p. 446, by original designation.

Remarks. The generic diagnosis of Palmer (1968, pp. B47, B48) is followed here.

Kootenia nodosa n. sp.

Fig. 13

Etymology. From Latin, *nodus*, swelling, referring to the median axial nodes on the pygidium.

Holotype. Pygidium, MGUH 21.258.

Material. More than 40 sclerites in GGU 298970–298973.

Diagnosis. Kootenia having moderately elongate cranidium. Glabella slightly expanding anteriorly; lateral furrows weak. Pygidium having five rings, a terminal piece, and a postaxial ridge in the axis; each axial ring with a small median node; pleural field with five furrows and four weak interpleural furrows; margin with six pairs of subequally spaced spines, first pair short and slender, others short and moderately wide.

Description. Cranidium moderately elongate, well-rounded anteriorly. Glabella strongly convex, slightly expanding anteriorly, slightly constricted at S1, distinctly constricted in front of fossulae; lateral glabellar furrows shallow, S1 geniculate, S2 transverse. Occipital ring with strong median spine. Anterior border narrow in front of glabella, slightly wider at sides. Anterior area of fixigena reduced to narrow depression between border and eye ridge. Eye ridge distinct. Posterior area of fixigena slightly more than one-half glabellar width. Palpebral lobe moderately long in small specimens but incomplete in large specimens. Surface with fine, densely spaced

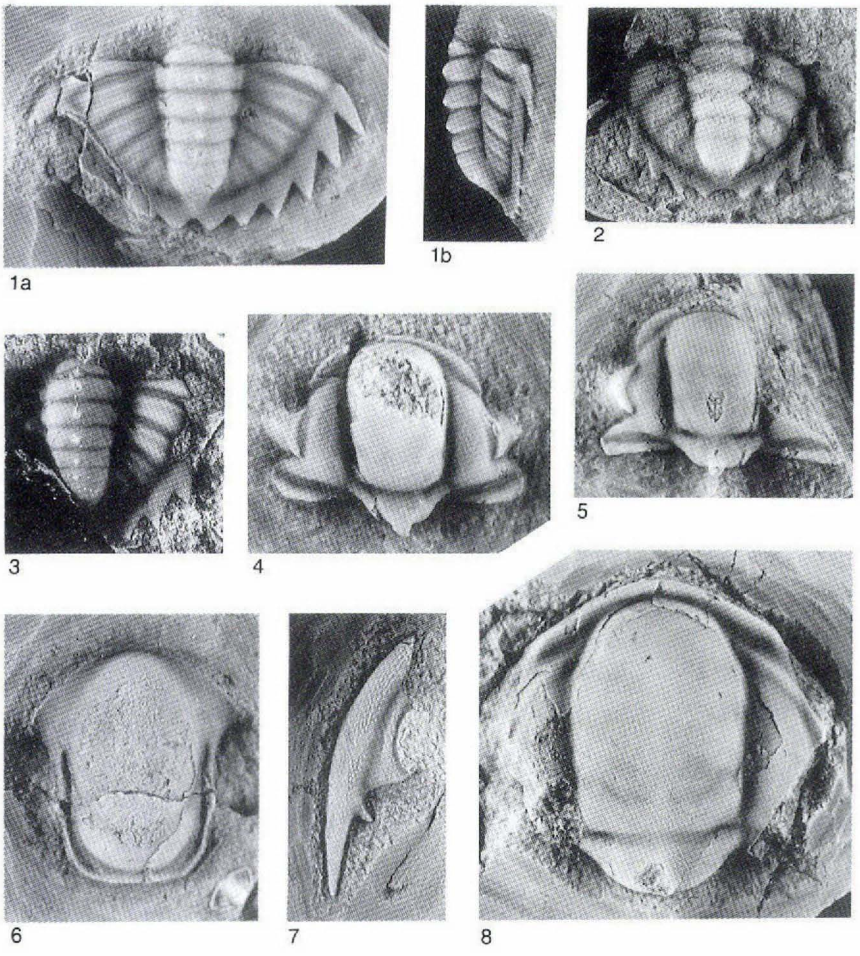


Fig. 13. *Kootenia nodosa* n. sp. All specimens from GGU 298970. 1, holotype pygidium in dorsal (a) and right-lateral (b) views, MGUH 21.258, × 5. 2, latex cast of weathered pygidium, MGUH 21.259, × 4. 3, latex cast of incomplete pygidium, MGUH 21.260, × 5. 4, small cranidium, MGUH 21.261, × 8. 5, small cranidium, MGUH 21.262, × 5. 6, labrum, MGUH 21.263, × 7; pygidium of *Glossopleura walcotti* Poulsen in lower right of photograph is the same specimen illustrated in Fig. 12.3. 7, librigena, MGUH 21.264, × 5. 8, large, incomplete cranidium, MGUH 21.265, × 4.5.

granules except in furrows and on anterior border; anterior border with terrace lines that parallel margin.

Thorax unknown.

Pygidium semicircular except for marginal spines. Axis convex, elevated well above pleural field, moderately tapering, having five rings, terminal piece, and short postaxial ridge extending to posterior margin; ring furrows shallowing posteriorly; each axial ring with small median node, decreasing in size posteriorly. Pleural field slightly convex, having five furrows that shallow posteriorly and four weak interpleural furrows. Border furrow shallow, wide. Margin with six pairs of spines, subequally spaced; first pair short and slender, remaining spines short, nearly uniform in length, moderately wide. Surface with fine, densely spaced granules except in furrows.

Remarks. Numerous species of *Kootenia* have been described from various localities worldwide but none is particularly similar to *K. nodosa* in the combination of pygidial characters. *K. nodosa* has a distinctive pygidium with five rings in the axis, each with a small median node of variable expression. Six pairs of short marginal spines are present. The first pair is slender and the rest are moderately wide. Another distinctive character of the pygidium is that five pairs of furrows and four pairs of weak interpleural furrows are present in the pleural region.

Occurrence. Common in wackestone approximately 42 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. It is associated with polymeroids indicative of the *Glossopleura* Assemblage-zone.

Genus *Olenoides* Meek, 1877

Olenoides Meek, 1877, p. 25; Kobayashi, 1935, pp. 152–154 (for synonymy to 1935); Lermontova, 1940, p. 138; Shimer & Shrock, 1944, p. 613; Ivshin, 1953, p. 37; Palmer, 1954, pp. 62, 63; Poulsen *in* Harrington *et al.*, 1959b, p. O218; Robison, 1964, p. 537; Robison, 1971, p. 799; Robison, 1988, p. 64; Young & Ludvigsen, 1989, p. 19

Neolenus Matthew, 1899, p. 52 (see Kobayashi, 1935 for synonymy to 1935); Lake, 1938, p. 260

Type species. Paradoxides(?) *nevadensis* Meek, 1870, p. 62, by original designation (Meek, 1877, p. 25).

Remarks. The generic diagnosis of Robison (1964, p. 537) is followed here.

Olenoides sp.

Fig. 14.1

Material. One nearly complete pygidium and one nearly complete cranidium, plus several cranidial and pygidial fragments, in GGU 298970.

Remarks. A distinctive species of *Olenoides* is represented by sclerites in GGU 298970. The cranidium is

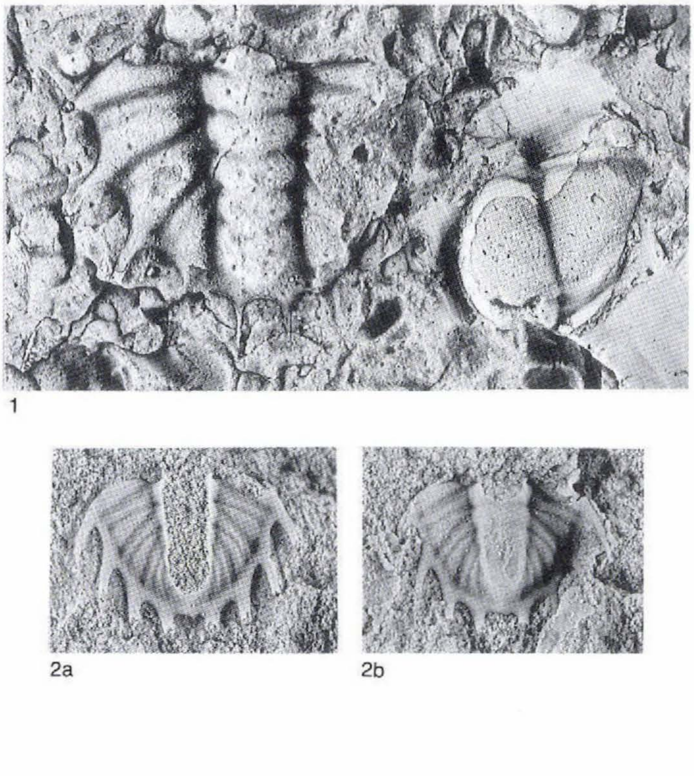


Fig. 14. Specimens of *Olenoides*.

1, *Olenoides* sp. Weathered bedding surface with broken pygidium (left), MGUH 21.266, and broken cranidium (right), MGUH 21.267, from GGU 298970, × 2.

2, *Olenoides* cf. *O. convexus* Rasetti; pygidium (a) and latex cast of counterpart (b), MGUH 21.268 from GGU 319789 (a) and 319790 (b), × 8.

known from only fragmentary, partially exfoliated specimens. The glabella is anteriorly expanding, moderately convex, and elevated well above the fixigena. It extends well past the anterolateral corner of the cranidium, and is unfurrowed except for a short, weak depression extending from each fossula. The occipital furrow is distinct. The occipital ring is broken, but evidently bore a medial spine. The fixigena is wide for the genus. Both the axial furrows and eye ridges are distinct. Surface prosopon appears to have been lacking except for terrace lines that parallel the margin, and which are present only on the anterior border.

The thorax is unknown, and the pygidium is known from only incomplete, exfoliated specimens. The axis is elevated well above the pleural field, and contains four rings and a long terminal piece. It is slightly tapered posteriorly, and has a minor constriction at the fourth ring. The ring furrows are strong. The first two axial rings both have a small median node. Other rings may have had median nodes, but all the specimens are broken. The pleural field is moderately convex, and has three strong, wide pleural furrows, and three weak interpleural furrows. Both pleural furrows and interpleural furrows become slightly shallower posteriorly. Marginal spines consist of five pairs that are subequally spaced and posteroradially disposed. The first four pairs evidently were long and slender. The last pair is moderately long, and about one-half the width of the preceding spines. Surface prosopon has not been observed.

Four described species of *Olenoides* have five pairs of marginal spines. They are *O. serratus* (Rominger, 1887) from the Stephen Formation of British Columbia and possibly boulder L-9, Ville Guay, Quebec (Rasetti, 1948b), *O. decorus* Resser, 1942, from the Marjum Formation of Utah, *O. superbus* (Walcott, 1908) from the Marjum Formation of Utah, and *O. aptus* Suvorova, 1964, from Siberia. The pygidium of the species from North Greenland most closely resembles the pygidium of *O. serratus*. It differs from both *O. serratus* and *O. decorus* in having longer marginal spines, a shorter terminal piece in the axis, and shallower interpleural furrows. It differs from *O. superbus* in having marginal spines of different lengths and two or three fewer axial rings. Differences in the pygidium that distinguish it from *O. aptus* are somewhat narrower pleural lobes, deeper pleural and interpleural furrows, a longer terminal piece in the axis, and marginal spines that project more radially.

Occurrence. Present in a packstone bed from approximately 56 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. It is associated with trilobites of the *Ptychagnostus gibbus* Interval-zone of Robison (1984).

Olenoides cf. *O. convexus* Rasetti, 1948b

Fig. 14.2

Olenoides convexus Rasetti, 1948b, p. 338, pl. 51, figs 5–9

Material. Two pygidia, one in GGU 319790, the other in GGU 319789 (part) and 319790 (counterpart).

Remarks. Two new pygidia are compared with *Olenoides convexus* Rasetti, 1948b, which was previously known from only boulder G-6, of Middle Cambrian age, from Grosses Roches, Quebec. An associated cranidium was not found. The best preserved pygidium (Fig. 14.2) is complete except for the ends of its marginal spines. It differs slightly from Rasetti's figured specimens in having marginal spines that are subequally spaced instead of slightly increasing in separation posteriorly. The ring furrows of both specimens are less well impressed than on specimens illustrated from Quebec. Characters of the pygidium that are diagnostic of *O. convexus*, including the presence of four pleural furrows, three interpleural furrows, and four pairs of marginal spines, each of which is offset slightly forward of its corresponding pleural furrow and is upwardly curved distally, are all present on the new specimens.

Occurrence. New material is from a packstone bed of the basal Kap Stanton Formation at locality 2, Nyeboe Land. It is associated with trilobites indicative of the *Ptychagnostus atavus* Interval-zone of Robison (1984).

Family Menomoniidae Walcott

Genus *Bolaspidella* Resser, 1937

Bolaspidella Resser, 1937b, p. 3; Robison, 1964, pp. 552–554 (for synonymy to 1964); Robison, 1971, p. 801; Shaw, 1966, p. 292; Palmer, 1968, p. B66; Öpik, 1967, p. 367; Öpik, 1970, p. 44; Shah & Sudan, 1982, p. 237; Robison, 1988, p. 79

Hysteropleura Raymond, 1937, p. 1094; Shaw, 1966, p. 290

Type species. Ptychoparia housensis Walcott, 1886, by original designation (Resser, 1937b, p. 3).

Remarks. Robison (1964, 1971, 1988) discussed the concept and content of *Bolaspidella*. That generic concept is followed here.

Bolaspidella sp.

Fig. 15

Material. One cranidium in GGU 298970.

Remarks. A single, small, mostly exfoliated cranidium is

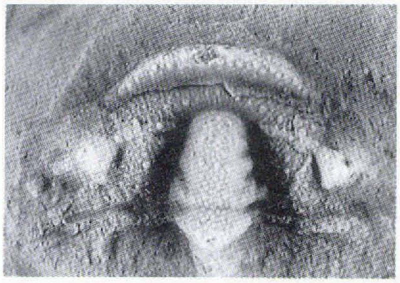


Fig. 15. *Bolaspidella* sp.; cranidium, mostly exfoliated, MGUH 21.269 from GGU 298970, × 10.

present in GGU 298970. Identification of the specimen to species is deferred until more material is available. The glabella is moderately tapered and bluntly rounded at the front. Three pairs of lateral glabellar furrows are well developed. Medially, the occipital ring is wide, and has a broken spine base. The anterior border is wider than the preglabellar field. The palpebral lobes are moderately long and located opposite the glabellar midpoint. Anteriorly, the facial suture is strongly convergent, and posteriorly, it is strongly divergent. Granules of bimodal size cover the entire cranidium, except in the furrows, and type 4 caeca radiate from the anterior and anterolateral areas of the axial furrow into the preglabellar field.

Occurrence. From a packstone bed approximately 56 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. It is associated with trilobites of the *Ptychagnostus gibbus* Interval-zone of Robison (1984).

Family Ogygopsidae Rasetti

Genus *Ogygopsis* Walcott, 1889

Ogygopsis Walcott, 1889, p. 466; Miller, 1892, p. 710; Grabau & Shimer, 1910, p. 289; Walcott, 1916, pp. 375, 376; Raymond & Walcott, 1937, p. 718; Shimer & Shrock, 1944, p. 613; Rasetti, 1951, p. 190; Rasetti *in* Harrington *et al.*, 1959b, p. O219; Nelson, 1963, pp. 244–247; Palmer, 1964, pp. F6, F7; Young & Ludvigsen, 1989, p. 19

Taxioura Resser, 1939b, p. 62; Shimer & Shrock, 1944, p. 617; Egorova *et al.*, 1960, p. 187

Type species. *Ogygia klotzi* Rominger, 1887, by original designation (Walcott, 1889, p. 466).

Remarks. The diagnosis of *Ogygopsis* followed here is that of Palmer (1964), who also provided a brief differential diagnosis of each species.

Ogygopsis klotzi (Rominger, 1887)

Fig. 16

Ogygia klotzi Rominger, 1887, p. 12, pl. 1, fig. 1

Ogygia? *klotzi* Walcott, 1888, p. 166

Ogygopsis klotzi Walcott, 1889, p. 446; Woodward, 1902, p. 530, text-fig. 1; Walcott, 1908, pl. 4, fig. 4; Grabau & Shimer, 1910, p. 289, fig. 1597; Walcott (in part), 1916, pp. 377, 378, pl. 66, figs 1, 1a (not 1b); Raymond & Walcott, 1937, fig. 1382; McLaughlin & Enbysk, 1950, p. 470, pl. 65, fig. 1; Rasetti, 1951, pp. 191, 192, pl. 12, figs 1–5, pl. 21, figs 1–3, pl. 29, figs 6–8; Rasetti *in* Harrington *et al.*, 1959b, p. O219, fig. 160,*1*; Nelson, 1963, pp. 244, 247; Palmer, 1964, pp. F6, F7; Hofmann & Parsley, 1966, pp. 209–211, text-fig. 2; Gupta (in part), 1967, p. 276, figs 1–3, 5, 9 (not 6); Campbell, 1971, pp. 437–440, pl. 52, figs 11, 12; Rudkin, 1979, fig. 1a-h; McNamara & Rudkin, 1984, pp. 164–168, figs 9, 10; Young & Ludvigsen, 1989, pp. 19, 20, pl. 5, fig. 11, pl. 6, figs 1–4, fig. 6C; Talent, 1990, p. 405

Ogygia (*Ogygopsis*) *klotzi* Rominger. Matthew, 1899, pp. 58, 59

?*Taxioura elongata* McLaughlin & Enbysk, 1950, pp. 470, 471, pl. 65, figs 2, 9

?*Taxioura*? sp. McLaughlin & Enbysk, 1950, p. 471, pl. 65, fig. 3

Ogygopsis klotzi? Stoyanow, 1958, pp. 349, 350, pl. 1, fig. 2

Holotype. Philadelphia Academy of Natural Sciences (*fide* Rasetti, 1951, p. 192), number unknown.

New material. One cranidium, two pygidia, and one librigena in GGU 298971–298973.

Remarks. New specimens of *Ogygopsis* from Nyeboe Land conform in all observed characters with figured or

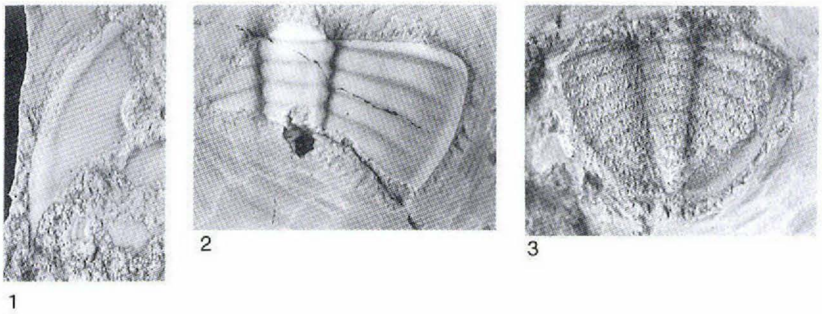


Fig. 16. *Ogygopsis klotzi* (Rominger). All specimens from GGU 298971. 1, latex cast of librigena, MGUH 21.270, × 2. 2, broken pygidium, MGUH 21.271, × 3. 3, weathered pygidium, MGUH 21.272, × 3.

examined specimens of *O. klotzi* from the Stephen Formation of British Columbia. The new specimens are all holaspides but are small compared to the maximum size obtained by specimens from British Columbia. Pygidia from Nyeboe Land have relatively weaker interpleural furrows than those from British Columbia. This character is variable, and probably influenced by compaction, and it is not considered to have taxonomic significance.

Specimens described by McLaughlin & Enbysk (1950) as *Taxioura elongata* and *Taxioura*? sp. from the Metalline Limestone of Pend Oreille County, Washington seem to belong to *O. klotzi*, judging from published illustrations. *O. klotzi* was also described from the Metalline (McLaughlin & Enbysk, 1950, p. 470), and I tentatively consider the three forms to be synonyms.

Occurrence. From wackestone approximately 42 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. Other unquestioned reports of *O. klotzi* are from British Columbia (Rasetti, 1951, pp. 191, 192), California, Nevada and Washington (Nelson, 1963, p. 247), Pennsylvania (Campbell, 1971, pp. 437, 438), and western Newfoundland (Young & Ludvigsen, 1989, pp. 19, 20). The total observed range of *O. klotzi* is from the upper part of the *Olenellus* Assemblage-zone to the *Oryctocephalus* Assemblage-zone (upper *Ptychagnostus praecurrens* Interval-zone of Robison, 1984). Nelson's (1963) statement that *O. klotzi* ranges into the upper Middle Cambrian seems to be erroneous.

A report of *O. klotzi* from Zachaldor, Kashmir, India (Gupta, 1967), seems to be in error. Talent (1990) demonstrated that five of six of Gupta's figures were copied from Rasetti (1951). The other figure (Gupta, 1967, fig. 6) appears to be part of the axial lobe of an indeterminate trilobite, but the axial rings are too narrow for the specimen to belong to *Ogygopsis*.

Family Paradoxididae Hawle & Corda

Remarks. Numerous discussions of the classification and evolution of paradoxidid trilobites have been published over the last 70 years. Some important opinions include those expressed by Howell (1933), Whitehouse (1939), Westergård (1950), Šnajdr (1957, 1958), Poulsen (*in* Harrington *et al.*, 1959b), Öpik (1961), and Bergström and Levi-Setti (1978).

Six genera of the family Paradoxididae (*sensu* Poulsen *in* Harrington *et al.*, 1959b) and two genera of the family Protolenidae (*sensu* Henningsmoen *in* Harrington *et al.*, 1959b), which are putatively closely related (Öpik, 1961), were analyzed cladistically using PAUP (Phylogenetic Analysis Using Parsimony; Swofford, 1989) to determine phylogenetic relationships among the taxa. The analyzed paradoxidids and protolenids are inferred to be a monophyletic (holophyletic) group (Fig. 17) united by the shared derivation of a distinctive, elongate palpebral lobe. Here, this monophyletic group is treated as the family Paradoxididae Hawle & Corda, 1847. It embraces, but is not restricted to, the genera *Xystridura*, *Galahetes*, *Lermontovia*, *Bergeroniellus*, *Paradoxides*, *Anopolenus*, *Clarella*, and *Centropleura*. Analyses were performed on a data matrix (Table 2) of equally weighted characters expressed in holaspides. All genera analyzed are known from relatively complete specimens. *Paradoxides* was used as a proxy for the group that also includes *Acadoparadoxides*, *Eccaparadoxides*, *Hydrocephalus*, and *Eoparadoxides*. Where there was ambiguity about character states present in a genus, characters in only the type species were analyzed. Transformation states were polarised using *Elrathia* as the primitive outgroup.

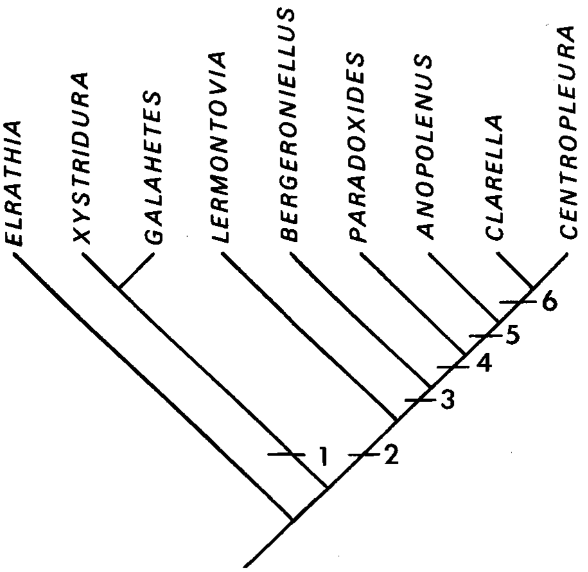


Fig. 17. Cladogram illustrating hypothesized phylogenetic relationships among selected genera of the family Paradoxididae, based on characters preserved in holaspides. *Elrathia* is used as the outgroup. Characters represented by character bars (numbered) are explained in the text.

An exhaustive search of genera in the Paradoxididae yielded one most parsimonious tree (Fig. 17). Within the Paradoxididae, two major clades seem to have arisen. One, the subfamily Xystridurinae Whitehouse, 1939, includes *Xystridura* and *Galahetes*. This group is united by the shared acquisition of a macropleural segment that is ankylosed to the pygidium rather than being shed forward into the posterior thorax as in other paradoxidids (Fig. 17, character bar 1). A large rostral plate is present in both *Xystridura* and *Galahetes*. It is either homoplasic with the

Table 2. Characters used to express relationships among paradoxidid trilobites

Characters and character states used to construct the cladogram expressing inferred relationships among paradoxidid trilobites (Fig. 17). Character states are those of holaspid specimens. A question mark indicates missing data.

1. Anterior glabella: not expanded (0); slightly expanded (1); greatly expanded (2).
2. Confluent S1 lateral glabellar furrow: absent (0); present (1).
3. Number of lateral glabellar furrows: 4 (0); 3 (1); 2 (2); 0 (3).
4. Anterior glabellar furrow: transverse (0); longitudinal (1).
5. Anterior branch of facial suture: divergent (0); retrodivergent (1).
6. Size of pygidium: small (0); micropygous (1); macropygous (2).
7. Number of pleurae in pygidium: greater than or equal to 3 (0); less than 3 (1).
8. Number of thoracic segments: less than or equal to 13 (0); 14 to 15 (1); 16 (2); 17 to 21 (3).
9. Size of rostral plate: medium (0); large (1); small (2).
10. Anterolateral spines on labrum: absent (0); present (1).
11. Pygidial border: present (0); absent (1).
12. Curvature of palpebral lobes: even (0); uneven (1).
13. Length of palpebral lobes: short (0); moderately long (1); very long (2); to rear of cranidium (3).
14. Metafixigenal spines: absent (0); present (1).
15. Macropleural segment in anterior thorax: absent (0); present (1).
16. Width of pleurae: wide (0); moderately reduced (1); much reduced (2).
17. Macropleural segments in posterior region: absent (0); ankylosed to pygidium (1); shed into thorax (2).
18. Eye ridges: present (0); absent (1).
19. Length of genal spines: less than or equal to one-half of body length (0); greater than one-half of body length (1).
20. Pleural lobes: convex (0); flat (1).
21. Axial spine in thorax: absent (0); present (1).
22. Preoccipital ridge: absent (0); present (1).
23. Medial nodes on pygidial axis: absent (0); present (1).
24. Maximum holaspid length: less than 7 cm (0); equal to or greater than 7 cm (1).

Genera	Characters				
		1	11111	11112	2222
	12345	67890	12345	67890	1234
Elrathia (outgroup)	00000	00000	00000	00000	0000
Centropleura	21011	20210	11210	22111	0001
Xystridura	10100	00011	10100	01000	0000
Paradoxides	21200	11301	10101	10100	0001
Bergeroniellus	00000	111?1	10100	10000	0000
Lermontovia	00100	113??	00100	00000	1100
Anopolenus	11011	201??	10300	221?1	0001
Clarella	21011	201??	11310	221?1	0001
Galahetes	20100	0001?	10110	01000	0010

rostral plate of *Centropleura* or symplesiomorphic. The sister group of the xystridurines includes the paradoxidines *Lermontovia*, *Bergeroniellus*, *Paradoxides*, *Anopolenus*, *Clarella*, and *Centropleura*. Previously, *Lermontovia* and *Bergeroniellus* were assigned (Henningsmoen *in* Harrington *et al.*, 1959b) to the subfamily Protoleninae Richter & Richter, 1948 of the family Protolenidae Richter & Richter, 1948 and *Anopolenus*, *Clarella*, and *Centropleura* were assigned to the subfamily Centropleurinae Angelin, 1854, of the family Paradoxididae. Herein, all these genera are considered to belong in the subfamily Paradoxidinae Hawle & Corda, 1847. The group shares an increased number of thoracic segments (14 or more), which is interpreted to be a peramorphic character (Fig. 17, character bar 2).

The subfamily Centropleurinae Angelin, 1854, with *Centropleura* as the nominal genus, is here considered to be a junior synonym of Paradoxidinae Hawle & Corda, 1847. Although *Anopolenus*, *Clarella*, and *Centropleura* seem to constitute a monophyletic group, retention of separate formal status for that group would result in the use of the name Paradoxidinae for a paraphyletic group including *Lermontovia*, *Bergeroniellus*, and *Paradoxides*.

Each of the character bars numbered 2 to 6 (Fig. 17) is supported by at least one character, although some characters are probably reductions from the inferred primitive condition for the paradoxidids. Character bar 2 represents the shared acquisition of 14 or more thoracic segments and a small pygidium. Character bar 3 represents a reduction in width of the pleurae. Character bar 4 represents the acquisition of a confluent S1 lateral glabellar furrow. The loss of eye ridges at this stage is probably an expression of paedomorphosis, but the heterochronic process that led to an increase of the adult length to greater than 7 cm is equivocal. Character bar 5 represents the acquisition of a longitudinal anterior glabellar furrow, a retrodivergent expression of the anterior branch of the facial suture, a backward extension of the palpebral lobe near or to the posterior border furrow (possibly through paedomorphosis), and the shedding of macropleural segments forward into the posterior thorax (probably an expression of peramorphosis). Other characters at character bar 5 are extreme reductions in width and convexity of the thoracic pleurae. Character bar 6 represents the acquisition of metafixigenal spines in holaspides. The character arose through paedomorphosis and was probably independently derived in *Galahetes*. That it arose through paedomorphosis is evident from the appearance of metafixigenal spines in the early ontogeny of *Xystridura*, *Galahetes*, and *Centropleura* and its loss in the later ontogeny of *Xystridura*. Extensive ontogenetic sequences are not known for either *Anopolenus* or *Clarella*, but it is inferred that they share basic similarities with the ontogeny of *Centropleura*.

Genus *Centropleura* Angelin, 1854

Centropleura Angelin, 1854, p. 87; Angelin, 1878, p. 87; Lindström, 1901, pp. 16, 24, 49; Grönwall, 1902, pp. 122, 123; Illing, 1916, p. 430; Howell, 1933, p. 216; Howell, 1937, p. 1170; Lake, 1934, pp. 187–189; Lermontova, 1940, p. 135; Shimer & Shrock, 1944, p. 609; Westergård, 1950, pp. 3, 4; Poulsen *in* Harrington *et al.*, 1959b, p. 0214; Öpik, 1961, p. 99; Lermontova *in* Chernysheva, 1960, p. 71; Suvorova, 1960, p. 71; Rasetti, 1967, p. 90

Anopolenus Salter. Kobayashi, 1935, p. 126

Luhops Šnajdr (in part), 1957, pp. 239, 244; Šnajdr (in part), 1958, pp. 152–153

Type species. *Paradoxides loveni* Angelin, 1851, p. 2, by monotypy (Angelin, 1854, p. 87).

Emended diagnosis. Cephalon semiparabolic in dorsal outline. Cranidium flattened except for strongly convex axis; anterior border wide, upturned; posterolateral corner rounded, usually with metafixigenal spine. Glabella strongly convex, forwardly expanding; S1, S2, S3 transverse, S4 oblique backward; L4 triangular. Palpebral lobe long, thin, arcuate, unevenly curved. Fixigena flat except for slightly raised genal bar and palpebral lobe. Librigena narrow; genal spine long, curved, divergent. Facial suture retrodivergent on anterior branch; broadly arcuate, divergent at eye; posterior branch concave, cutting posterior border between genal and metafixigenal spines. Labrum subquadrate, anterior border strongly curved, anterior wings short, posterior wings short to long. Rostral plate large, broadly curved, narrow medially and widening distally.

Thorax having 16 segments, strongly convex axially, flattened pleurally. Axial furrow well defined. Segments 1 to 13 narrower than cranidium; axial rings wide, convex; pleural furrows shallow, oblique; segments terminating in short to moderately long pleural spines. Segments 14 to 16 hypertrophic, falcate.

Pygidium short, wide, flattened except for axis. Pleural field wide, having 2 or 3 pairs of short marginal spines.

Remarks. Westergård (1950) reviewed the taxonomic history of *Centropleura* and the closely related genera *Anopolenus* and *Clarella*. Although the morphological differences among these taxa seem to be relatively minor, I continue to recognise each as an independent genus rather than recognising *Anopolenus* and *Clarella* as subgenera of *Centropleura* as Öpik (1961) did. Šnajdr (1957) erected the paradoxidid genus *Luhops* with *Paradoxides expectans* Barrande, 1852, as the type species. Öpik (1961, pp. 103, 104), however, indicated that Šnajdr had combined cranidia of *Paradoxides* or *Hydrocephalus* with pygidia and a thorax of *Centropleura* in his concept of Barrande's (1852) species. After examination of casts of some of Šnajdr's (1958) illustrated specimens (USNM 90831), I concur with Öpik's conclusion. Illustrated material of *C.* (*Beishanella*) *beishanensis* Xiang & Zhang, 1985, the type species of the subgenus, is not sufficient to determine whether or not continued use of the subgeneric name is warranted.

Centropleura was widespread during the Middle Cambrian, possibly because it had a pelagic lifestyle (see Fortey, 1985). Characters supporting a pelagic existence (Fortey, 1985; Babcock in press) include strongly reduced pleural areas, an inflated glabella, the presence of numerous terrace lines on the dorsal surface, large eyes, and elongate marginal spines. Dispersal and adaptive radiation in the genus are inferred to have taken place in marine waters below the thermocline.

As presently defined, *Centropleura* includes the species *C. loveni* (Angelin, 1851), from Scandinavia, Bennett Island, and North Greenland; *C. angelini* Westergård, 1950, from Sweden and possibly North Greenland and Tien Shan; *C. angustata* Westergård, 1950, from Sweden; *C. belli* Hutchinson, 1952, from Quebec; *C. expectans* Barrande, 1852, from Bohemia; *C. keguqinensis* Xiang & Zhang, 1985, from Tien Shan; *C. oriens* Chernysheva, 1953, from Siberia; *C. phoenix* Öpik, 1961, from Queensland, Australia; *C. pugnax* Illing, 1916, from England; *C. sibirica* Lermontova, 1940, from Siberia; *C. sonax* Öpik, 1961, from Queensland, Australia; *C. tianshanensis* Xiang & Zhang, 1985, from Tien Shan; and *C. vermontensis* Howell, 1932, from Vermont. *C.* (*Beishanella*) *beishanensis* Xiang & Zhang, 1985 is from Tien Shan. *C. neglecta* Öpik, 1949, is known from only one fragmentary cranidium from Victoria, Australia. Evidence that it should be retained in *Centropleura* is inconclusive. Some other described occurrences of *Centropleura* include specimens unassigned to species from central Nevada (Stewart & Palmer, 1967; Palmer & Stewart, 1968; Babcock, 1990a), New York (Rasetti, 1967), the Altai region of Russia (Romanenko, 1985), Tasmania (Jago, 1972a, 1990), and northern Victoria Land, Antarctica (Cooper *et al.*, 1976, 1983). Its observed stratigraphic range is from the *Ptychagnostus atavus* Zone to the *Lejopyge laevigata* Zone.

Centropleura loveni (Angelin, 1851)

Figs 18, 19, 20.1–6

Paradoxides loveni Angelin (in part), 1851, p. 2, pl. 3, figs 1–3

Centropleura loveni (Angelin). Angelin (in part), 1854, p. 87; Angelin (in part), 1878, p. 95, pl. 3, fig. 1, 1a; Grönwall,

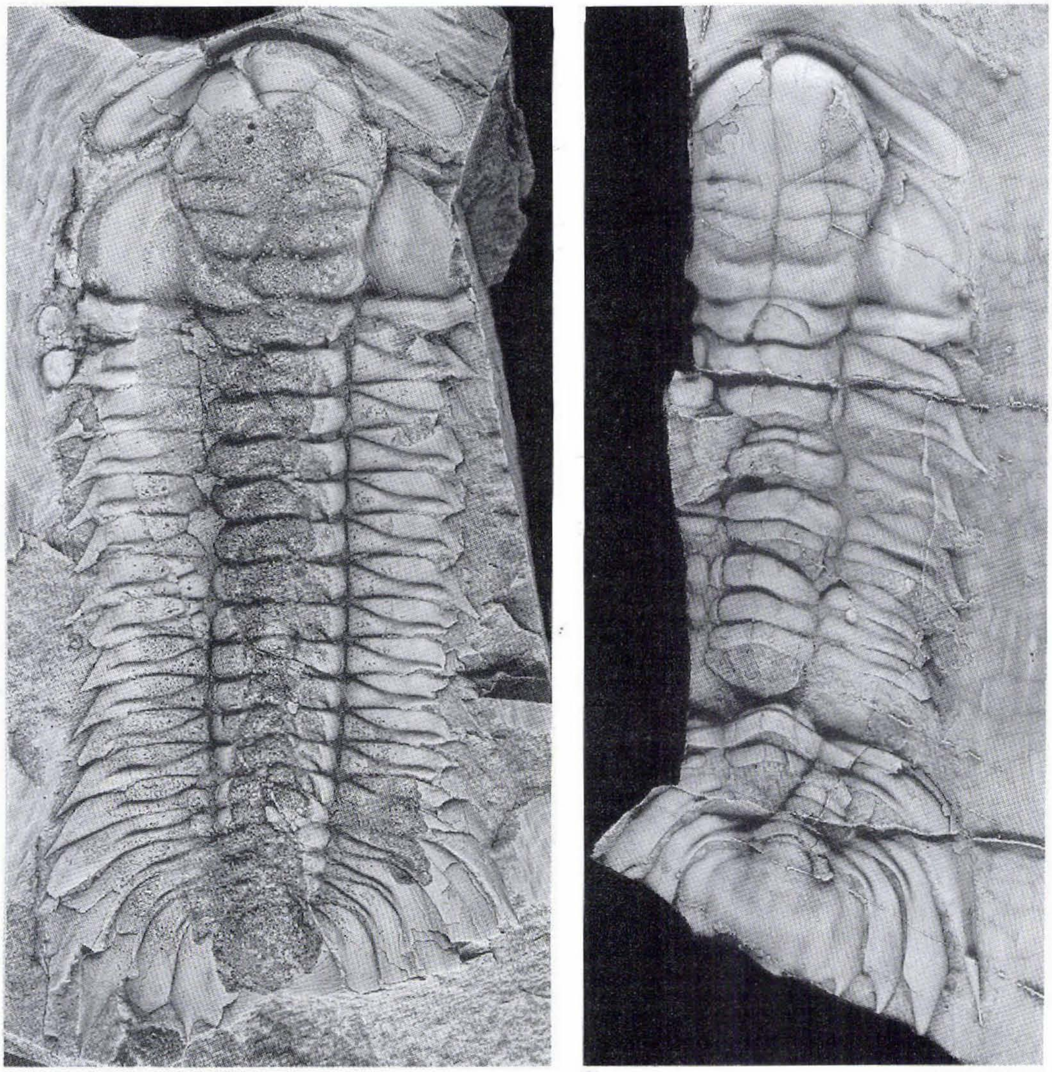


Fig. 18. *Centropleura loveni* (Angelin).
1, axial shield, weathered along the middle, MGUH 21.273 from GGU 301313, × 1.25; an agnostoid trilobite, *Toragnostus bituberculatus* (Angelin), is near the left side. 2, latex cast of slightly disarticulated axial shield, MGUH 21.083 from GGU 301312, × 1.25; a neoplasm (tumor) is on the right pleural area of the sixth thoracic segment (see Babcock 1993: figs 3.1, 3.2).

1902, pp. 124, 125;; Lermontova, 1940, p. 135, pl. 41, figs 2–4; Holm & Westergård, 1930, p. 16, pl. 3, figs 13–16, pl. 4, figs 24–25; Westergård (in part), 1950, pp. 4, 5, pl. 1, figs 1–3 (not 4), pl. 2, fig. 2?, (not 1); Poulsen (in part) *in* Harrington *et al.*, 1959b, p. O214, fig. 154*a* (not 154*b*); Reyment (in part), 1980, p. 7, fig. 15c (copy of Angelin, 1851, pl. 3, fig. 1) (not 15a?, 15b); Babcock, 1993, figs 3.1, 3.2

Centropleura angelini Westergård (in part), 1950, pp. 4–6, pl. 1, fig. 10

Lectotype. Angelin (1851, p. 2) based the type species of *Centropleura*, *Paradoxides loveni*, on an unknown number of specimens now in the Swedish Museum of Natural History and the Paleontological Museum, Uppsala University. His figures (Angelin, 1851, pl. 3, figs 1–3; one reproduced by Reyment, 1980, fig. 15c) of *C. loveni* are composites and include characters of *C. loveni*, *C. angelini* Westergård, 1950, and probably *Paradoxides*. Westergård (1950) recognised that two species of *Centropleura* were present in Angelin's collections and referred some specimens to his new species *C. angelini*. The only specimen from Angelin's material that was figured by Westergård (1950, pl. 1, fig. 1) and identified as *C. loveni* (RM Ar. 32354) is here selected as the lectotype. It is a small, fragmentary cranidium.

New material. Numerous disarticulated sclerites and three articulated axial shields in GGU 301311–301313 and 313115.

Emended diagnosis. Cranidium about 1.4 times wider than long. Exsagittal parts of anterior border with slight inward deflections in large holaspides; deflection lacking in small holaspides. Anterior border furrow deep and narrow anteriorly, shallowing and widening laterally. Axial furrow deep and narrow anteriorly, shallowing and widening posteriorly. Glabella pyriform, elevated well above fixigenae, reaching greatest width at L4, reaching greatest height in center of L5, sloping steeply forward to anterior border furrow and gently backward to occipital furrow. Lateral glabellar furrows shallowing anteriorly; S1 confluent, composite; S2 nearly straight, slightly oblique backward; S3 slightly convex, transverse; S4 slightly convex. Occipital furrow deep at sides, shallowing medially. Occipital ring lacking node. Fixigena with small metafixigenal spine near posterolateral end of border. Posterior margin and posterior border furrow strongly deflected on axial side of spine. Palpebral lobe not extending to posterior border furrow. Genal bar slightly bowed laterally.

Labrum slightly wider than long, moderately convex; having nearly straight, tapering lateral margin. Posterior wing long, truncated, slightly deflected in middle.

Thorax narrowest at segment 9, axis slightly tapering posteriorly. Anterior segments (1 to 13) having pleural spines that successively increase in length toward posterior. Segments 14 to 16 having curved anterior and posterior margins; pleural tips extending beyond pygidium, extension decreasing posteriorly from segment 14.

Pygidium bell-shaped, width about 1.5 times length. Anterior margin slightly curved; anterolateral corner broadly rounded; lateral margin slightly curved, diverging posteriorly. Axis having 2 or 3 rings and terminal piece, moderate to strongly tapered posteriorly. Posterior margin having 3 pairs of spines, length decreasing adaxially; spine pairs 1 and 2 posteromedially directed; spine pair 3 very short, posteriorly directed. Pleural furrows consisting of 3 shallow, wide pairs, weakening posteriorly.

Terrace lines cover dorsal surface except palpebral lobe, palpebral area of fixigena, anterior border furrow of cranidium, and axial furrows; strong except on glabella and anterior margin of axial rings away from middle. Terrace lines also present ventrally on marginal areas and labrum.

Remarks. Well-preserved, but somewhat crushed, specimens referable to *C. loveni* are present in the lower Kap Stanton Formation of North Greenland. Except for differences attributable to crushing, these specimens are identical to inflated specimens from Sweden and Denmark, some of which are introduced here for comparison (Figs 19.11, 20.3).

Angelin (1851) included representatives of two species of *Centropleura* in his concept of *C. loveni* from the Andrarum Limestone of Scania, Sweden (Westergård, 1950). Characters that can be used to differentiate the two species are primarily in the cranidium. The name *C. loveni* has been restricted to cranidia that have palpebral lobes not extending to the posterior border furrow, and that have the posterior margin and border furrow forwardly bent near the posterolateral corner (Westergård, 1950). Cranidia that have the palpebral lobes extending to the border furrow, a nearly straight posterior margin, and a nearly straight border furrow, belong to *C. angelini*.

Morphologically different pygidia also have been found in the Andrarum Limestone. One morph tends to have an elliptical outline (Fig. 20.7; Westergård, 1950, pl. 1, fig. 4) and another tends to have a bell-shaped outline (Fig. 20.3, Westergård, 1950, pl. 1, fig. 10a). As no complete specimens of either species were known at the time of Westergård's writing, the pygidia could not be assigned with certainty to their proper cranidia. Complete, articulated specimens of *C. loveni* from North Greenland (Fig. 18) show that Westergård incorrectly assigned elliptically shaped pygidia to *C. loveni*. By implication, he also incorrectly assigned bell-shaped pygidia to *C. angelini*.

Whether or not the rostral plate of *C. loveni* was fused to the labrum is uncertain. A disarticulated rostral plate from North Greenland (Fig. 20.2) seems to have been cleanly separated from the labrum medially, but fragments of exoskeleton appear to adhere to the distal margins. Illustrated labra of *Centropleura* that are free of the dorsal exoskeleton (Westergård, 1950, pl. 2, figs 2, 3; herein, Fig. 20.5) are also free of the rostral plate, suggesting that the labrum and rostral plate were either unfused or weakly ankylosed.

Ontogeny and heterochrony. New material of *C. loveni* from North Greenland and Scandinavia (Figs 18, 19, 20.1, 20.3, 20.4) provides substantially more information about the ontogeny of this species than has been previously known. Small cranidia (Figs 19.1–19.7) show a remarkable resemblance in overall morphology to meraspides or small holaspides of *Xystridura templetonensis* (compare with specimens figured by Öpik, 1975). This supports monophyly in the paradoxidids and furthermore suggests that major morphological innovations in the cranidium of *Centropleura* arose through paedomorphosis from the common ancestor of the two major paradoxidid clades. Critical points of comparison are (1) the facial sutures, which are deeply incised in meraspides of

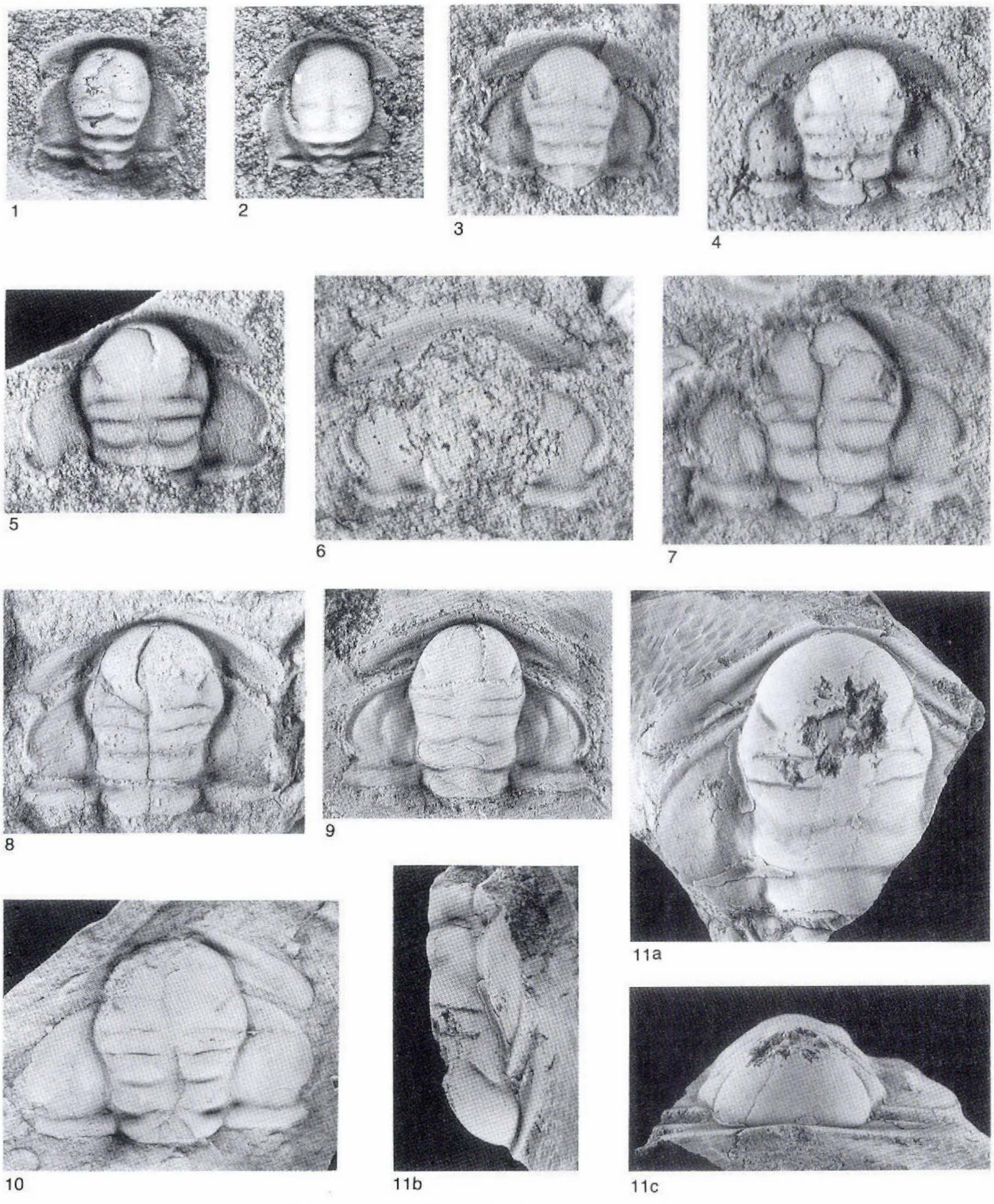


Fig. 19. *Centropleura loveni* (Angelin). All specimens from GGU 301313, unless otherwise stated.
1–5, small cranidia, MGUH 21.274–21.278, respectively, all × 10. 6, small, damaged cranidium, MGUH 21.279, × 8. 7, small, crushed cranidium, MGUH 21.280, × 8. 8, cranidium, MGUH 21.281, × 3. 9, medium-sized cranidium from the Andrarum Limestone of Andrarum, Scania, Sweden; introduced for comparison; USNM 465519, × 3. 10, cranidium, MGUH 21.282, × 1.5. 11, large, exfoliated cranidium in dorsal (a), left-lateral (b), and frontal views from the Andrarum Limestone of Andrarum, Scania, Sweden; introduced for comparison; USNM 465520, × 1.

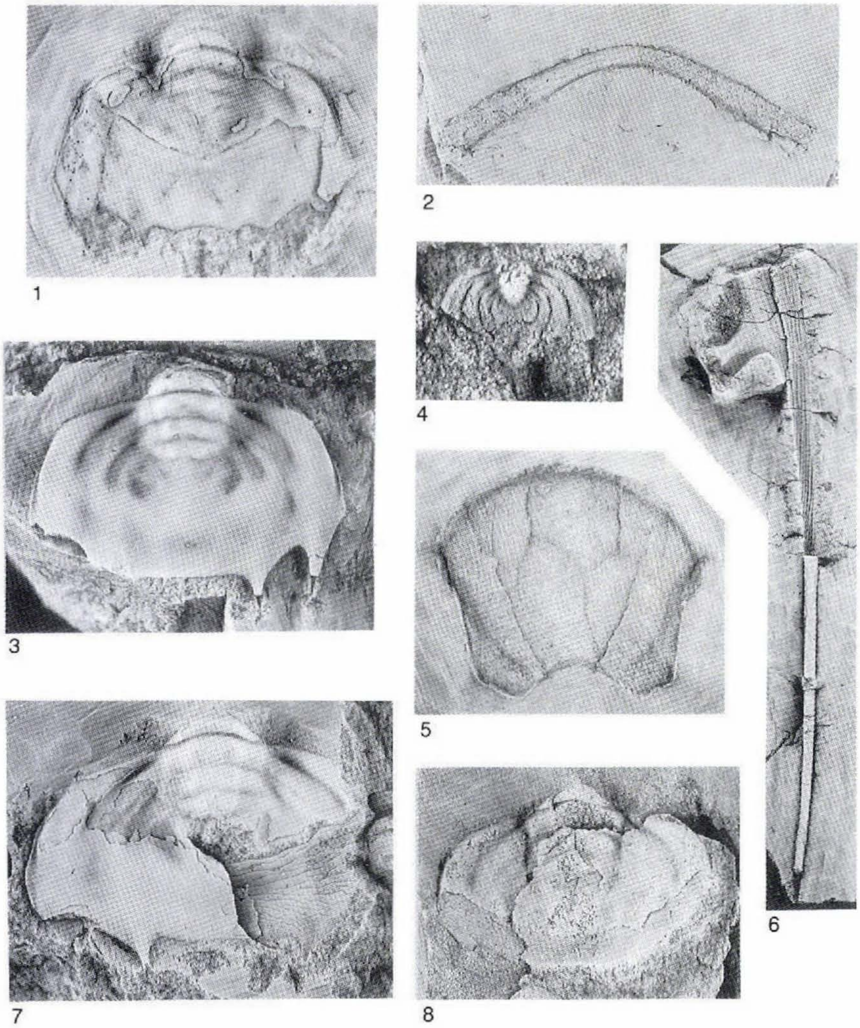


Fig. 20. Specimens of *Centropleura*.

1–6, *Centropleura loveni* (Angelin). 1, pygidium, mostly exfoliated, MGUH 21.283 from GGU 313115, × 2. 2, weathered rostral plate, MGUH 21.284 from GGU 313115, × 1. 3, pygidium, from Borregård, Bornholm, Denmark; introduced for comparison; USNM 465521, × 2.5. 4, smallest observed pygidium, MGUH 21.285 from GGU 301313, × 12. 5, labrum, MGUH 21.286 from GGU 313115, × 2. 6, incomplete librigena retaining much of the genal spine, preserved mostly as an external mould, MGUH 21.287 from GGU 301313, × 1.

7, *Centropleura angelini* Westergård; incomplete pygidium from the Andrarum Limestone, Andrarum, Scania, Sweden; introduced for comparison; USNM 465522, × 2.

8, *Centropleura angelini*? Westergård; pygidium, mostly exfoliated, MGUH 21.288 from GGU 301313, × 2.5.

both genera and become retrodivergent in holaspides of *Centropleura*; (2) the genal bars, which are lost in holaspides of *Xystridura* but not *Centropleura*; and (3) the metafixigenal spines, which are lost early in meraspid ontogeny by *Xystridura* but are retained by holaspides of *Centropleura*. Both genera evidently underwent protraction and retraction (see McNamara, 1986b) of the anterior glabella during the late meraspid or holaspid period, but *C. loveni* seems to have undergone more than *X. templetonensis*.

As discussed in remarks on the Paradoxididae, *Centropleura* has characters in the post-cephalic area that suggest a peramorphic origin.

Occurrence. Disarticulated sclerites and articulated axial shields are moderately common in mudstone beds of the basal Kap Stanton Formation at locality 3, Peary Land. Besides North Greenland, *C. loveni* has been reported from Sweden, Denmark, and Bennett Island. Its observed range is confined to the informal lower part of the *Lejopyge laevigata* Zone of Robison (1984).

Centropleura angelini? Westergård, 1950

Fig. 20.8

Centropleura loveni Angelin. Angelin (in part), 1854, p. 87; Angelin (in part), 1878, p. 95, pl. 3, figs 1, 1a; Westergård (in part), 1950, pp. 4, 5, pl. 1, fig. 4; pl. 2, figs 1, 3?; Poulsen (in part) *in* Harrington *et al.*, 1959b, p. O214, fig. 154*b*; Reyment (in part), 1980, figs 15a?, 15b

Centropleura angelini Westergård (in part), 1950, p. 6, pl. 1, figs 5–9 (not 10)

Holotype. Cranidium, RM Ar. 1617.

Material. One pygidium in GGU 301313.

Remarks. A single, mostly exfoliated pygidium of *Centropleura* in GGU 301313 seems to fall within the range of variation of *C. angelini* as herein revised (see remarks under *C. loveni*). The pygidium is much wider than long and has a roughly elliptical outline. A specimen referred to *C. angelini* from the Andrarum Limestone of Sweden is illustrated for comparison (Fig. 20.7). The identification of the specimen from North Greenland is questionable because a cranidium referable to *C. angelini* was not found in any collection from North Greenland, and because examination of pygidia referable to *C. loveni* from Scandinavia and North Greenland has shown considerable variation in outline of the pygidium.

Occurrence. Present in mudstone beds of the basal Kap Stanton Formation at locality 3, Peary Land. Besides North Greenland, *C. angelini* is also known from Scandinavia. Specimens definitely referable to *C. angelini* are from the informal lower part of the *Lejopyge laevigata* Zone of Robison (1984).

Family Solenopleuridae Angelin

Genus *Parasolenopleura* Westergård, 1953

Liostracus Angelin (in part), 1854, p. 27; Angelin (in part), 1878, p. 27

Parasolenopleura Westergård, 1953, pp. 21, 22; Poulsen *in* Harrington *et al.*, 1959b, p. O275; Rushton, 1966, pp. 46, 47

Type species. *Calymene aculeata* Angelin, 1851, pp. 23, 24 (not Poletaeva, 1955), by original designation (Westergård, 1953, p. 21).

Remarks. The generic concept of Westergård (1953, pp. 21, 22) is followed here.

Parasolenopleura aculeata (Angelin, 1851)

Fig. 21

Calymene aculeata Angelin, 1851, p. 23, pl. 19, fig. 2; Angelin, 1878, p. 23, pl. 19, fig. 2

Liostracus aculeatus (Angelin). Angelin, 1854, p. 27; Angelin, 1878, p. 27, pl. 19, fig. 2; Linnarsson, 1879, p. 11, pl. 1, figs 12–15; Linnarsson, 1883, p. 22; Walcott, 1884, pl. 6, fig. 6; Lesley, 1889, p. 351, fig.; Walcott, 1913, p. 137, pl. 13, fig. 6; Krashopeeva, 1958, p. 109; Strand, 1929, p. 351, pl. 2, fig. 5; ?Brøgger, 1878, p. 46 (30), pl. 3, fig. 3 (cf. *Parasolenopleura spinigera* Westergård, *fide* Westergård, 1953, p. 23)

Andrarina aculeatus (Angelin). Raymond, 1937, p. 1106

Parasolenopleura aculeata (Angelin). Westergård, 1953, pp. 23–25, pl. 5, figs 6–10, pl. 6, figs 1–4; Poulsen *in* Harrington *et al.*, 1959b, p. O275, fig. 204,*12*

Parasolenopleura cf. *aculeata* (Angelin). Rushton, 1966, p. 47, pl. 6, fig. 14; Morris, 1988, p. 168

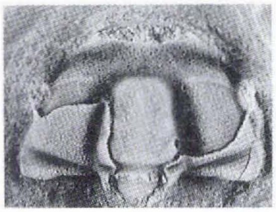


Fig. 21. *Parasolenopleura aculeata* (Angelin); partly exfoliated cranidium, MGUH 21.289 from GGU 298969, × 7.

Lectotype. Cranidium, RM Ar. 46143a.

New material. One cranidium in GGU 298969.

Remarks. The species concept of Westergård (1953, pp. 23, 24) is followed here. The new specimen from Nyeboe Land (Fig. 21) is a mostly exfoliated cranidium with a broken anterior border and occipital ring. It agrees in all characters with specimens figured by Westergård (1953) and, although slightly younger than that material, does not add new morphological information about the species.

Westergård (1953, p. 24) noted that the surface granulation in this species is a variable character. The new specimen from North Greenland has fine, densely spaced granules similar to specimens illustrated (Westergård, 1953, pl. 6, figs 3, 4) from the Exsulans Limestone of Scania, Sweden.

Occurrence. Present in mudstone of the upper part of the Henson Gletscher Formation at locality 1, Nyeboe Land. Specimens examined by Angelin (1851) are from the *Acrothele* (*Redlichella*) *granulata* conglomerate of Borgholm, Sweden. Those specimens and the ones reported by Westergård (1953) from Sweden and Norway are from the *Ptychagnostus gibbus* Interval-zone. A specimen compared with this species by Rushton (1966) was found in a loose block that may have come from the Purley shales. The Purley shales of England contain a fauna indicative of the *P. gibbus* Interval-zone. The new specimen from North Greenland extends the range of this species up to the *P. atavus* Interval-zone.

Genus *Solenopleura* Angelin, 1854

Solenopleura Angelin, 1854, p. 26; Salter, 1866, p. 305; Angelin, 1878, p. 26; Salter, 1881, p. 499; Walcott, 1884, p. 36; Matthew, 1887, p. 357; Miller, 1889, p. 567; Beecher, 1895, p. 178; Pompeckj, 1896, p. 546; Beecher, 1897, p. 192; Lindström, 1901, p. 25; Grabau & Shimer, 1910, p. 277; Vogdes, 1925, p. 113; Lake, 1931, p. 133; Kobayashi, 1935, p. 262; Howell, 1937, p. 1173; Lermontova, 1940, p. 151; Ivshin, 1953, p. 93; Chernysheva, 1953, p. 34; Westergård,

1953, pp. 7–11; Hupé, 1955, p. 137; Poulsen *in* Harrington *et al.*, 1959b, p. O275; Egorova *et al.*, 1960, pp. 231, 232; Ivshin *et al. in* Chernysheva, 1960, p. 119; Chernysheva, 1961, p. 242; Palmer & Gatehouse, 1972, p. D25; Chernysheva, 1980, pp. 65–67, 72, 73
Calymene Brongniart (in part). Angelin, 1878, pp. 22, 23
Jincella Šnajdr, 1957, p. 244; Šnajdr, 1958, p. 196

Type species. *Calymene holometopa* Angelin, 1851, p. 23, by subsequent designation (Walcott, 1884, p. 36).

Remarks. The generic concept of *Solenopleura* and arguments relating to its type species were discussed by Chernysheva (1980). Her diagnosis of the genus is followed here.

Solenopleura bucculenta Grönwall, 1902
Fig. 22

Solenopleura bucculenta Grönwall, 1902, pp. 152, 153, pl. 4, fig. 18; Czarnocki, 1927, p. 196; Westergård, 1953, pp. 13, 14, pl. 3, figs 1–3
Solenopleura cf. *bucculenta* Grönwall. Cobbold *in* Cobbold & Pocock, 1934, p. 366, pl. 42, fig. 18a, b; Morris, 1988, p. 212

Holotype. Repository unknown.

New material. Numerous disarticulated sclerites and articulated exoskeletons in GGU 301313 and 313115.

Remarks. Until now, *S. bucculenta* has been known from only cranidia, which were thoroughly described by Westergård (1953, pp. 13, 14). For comparison with new material from North Greenland, two specimens from Scandinavia are illustrated here (Figs 22.7, 22.9).

Specimens from North Greenland add new information about sclerites other than the cranidium. The librigena (Fig. 22.5) is narrow, moderately convex, and has a semicircular outline. Its border is wide and convex and the border furrow is deep and wide. An incipient spine is

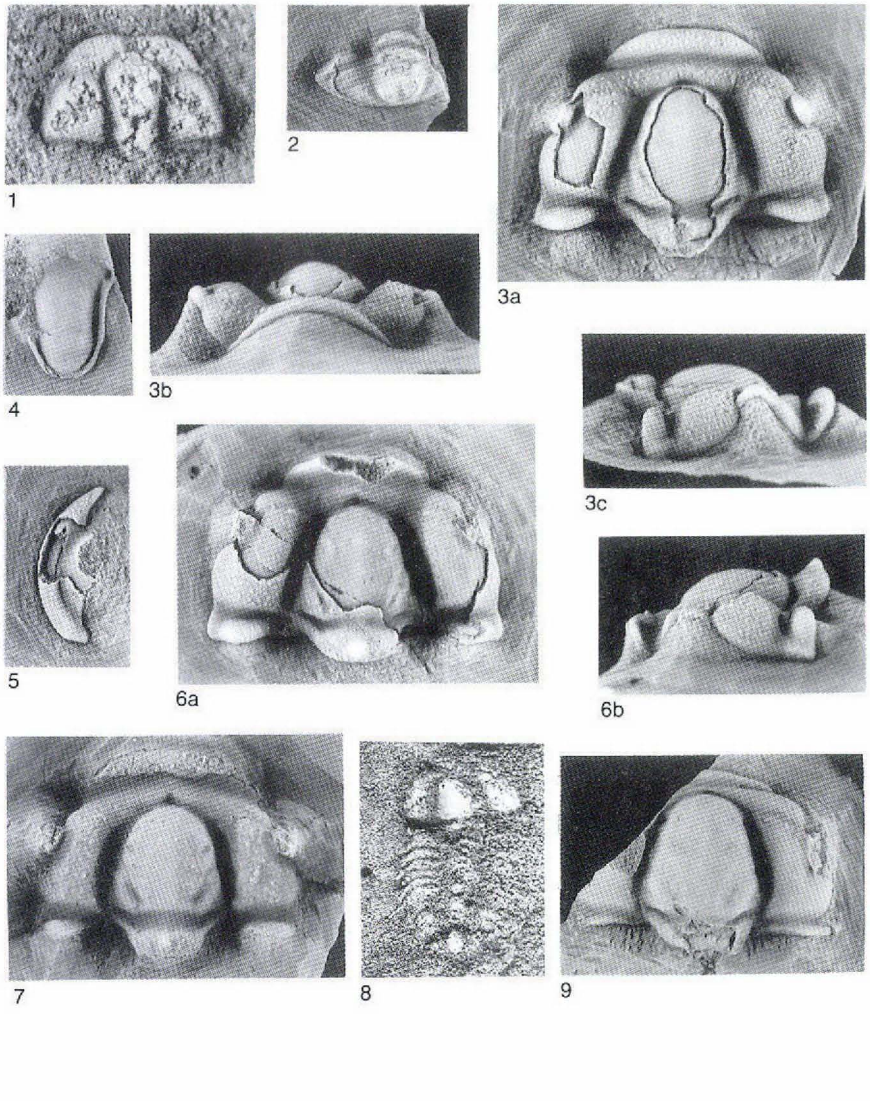


Fig. 22. *Solenopleura bucculenta* Grönwall. All specimens from GGU 301313, unless otherwise stated.
1, small cranidium, MGUH 21.290, × 16. 2, incomplete pygidium, mostly exfoliated, MGUH 21.291, × 3. 3, partly exfoliated cranidium in dorsal (a), frontal (b), and right-lateral (c) views, MGUH 21.292, × 3. 4, incomplete labrum, MGUH 21.293, × 3. 5, incomplete librigena, MGUH 21.294, × 3. 6, partly exfoliated cranidium in dorsal (a) and left-lateral (b) views, MGUH 21.295, × 3. 7, exfoliated cranidium from the Andrarum Limestone of Andrarum, Scania, Sweden; introduced for comparison; USNM 465523, × 3. 8, weathered axial shield, MGUH 21.296 from GGU 313115, × 1.5. 9, large cranidium, incomplete and exfoliated, from Øleå, Bornholm, Denmark; introduced for comparison; USNM 465524, × 1.25.

present at the genal angle. Surface prosopon consists of rather widely spaced, large granules between which are smaller, densely spaced granules. Granules are absent in the border furrow.

The labrum is known from a single broken specimen (Fig. 22.4). It is long, relatively narrow, and convex. The border is convex and separated from the central body by a deep and narrow furrow. The anterolateral corners are not preserved.

Several axial shields are in collection 313115 but, because of weathering, few details are preserved. At least ten segments are in the thorax, and most appear to have falcate tips (Fig. 22.8).

The best available pygidium (Fig. 22.2) is mostly exfoliated. It is moderately convex, and has a width that is about twice the length. The axis is strongly convex, and contains two rings and a long terminal piece that extends almost to the posterior margin. A weak medial groove extends the entire length of the terminal piece in the steinkern. The axis is widest at the second ring, and tapers slightly both anteriorly and posteriorly. Two distinct ridges and two weak interpleural furrows are in the pleural lobes. A border is not present. Test adheres to the internal mould only near the anterolateral corner, showing surface prosopon of small, densely spaced granules. Large granules like those on the cephalon are evidently absent from the pygidium.

Occurrence. Common in mudstone beds of the basal Kap Stanton Formation at locality 3, Peary Land. The species seems to range from the *Ptychagnostus punctuosus* Zone to the *Lejopyge laevigata* Zone of Robison (1984). Specimens described by Westergård (1953) from Sweden and Denmark are from the *Paradoxides davidis* Zone and the lower part of the *Lejopyge laevigata* Interval-zone. Specimens compared with this species (Cobbold *in* Cobbold & Pocock, 1934, p. 366) from Rushton, Shropshire, England, are from the *Paradoxides forchhammeri* Zone, which probably corresponds to about the same interval (*P. punctuosus* Zone to lower *L. laevigata* Zone).

Genus *Solenopleurella* Poulsen, 1927

Solenopleurella Poulsen, 1927, p. 269; Shimer & Shrock, 1944, p. 617; Lermontova, 1951, pp. 132–133; Rasetti, 1951, pp. 240, 241; Poulsen *in* Harrington *et al.*, 1959b, p. O275; Egorova *et al.*, 1960, p. 232; Ivshin *et al. in* Chernysheva, 1960, p. 119; Rasetti, 1965, p. 1013

Type species. *Solenopleurella ulrichi* Poulsen, 1927, by original designation (Poulsen, 1927, p. 269).

Remarks. The generic concept of Poulsen (*in* Harrington *et al.*, 1959b, p. O275) is followed here.

Solenopleurella transversa? Rasetti, 1965

Fig. 23

Solenopleurella transversa Rasetti, 1965, p. 1014, pl. 120, figs 22, 23

Holotype. Cranidium, USNM 145034.

New material. One cranidium in GGU 319790.

Remarks. This species was described (Rasetti, 1965) on the basis of a single broken cranidium from central Pennsylvania. A cranidium from Nyeboe Land is questionably assigned to this species because it agrees with the holotype in all critical characters. Aside from a difference in size, the new specimen (Fig. 23) differs from the holotype by having a slightly shorter palpebral lobe, and differences in surface granulation. The holotype has very low granules that are fine and closely spaced on the anterior border, moderately spaced on the occipital ring, and coarse and moderately spaced on the palpebral area of the fixigena. The specimen from North Greenland has granules of bimodal size on the fixigena. Such characters are variable within species of other solenopleurid trilobites and are here given no taxonomic significance.

The Greenland specimen shows two well-impressed pairs of lateral glabellar furrows and a third pair that is faintly impressed. Although Rasetti (1965) reported only two pairs of furrows, re-examination of the holotype

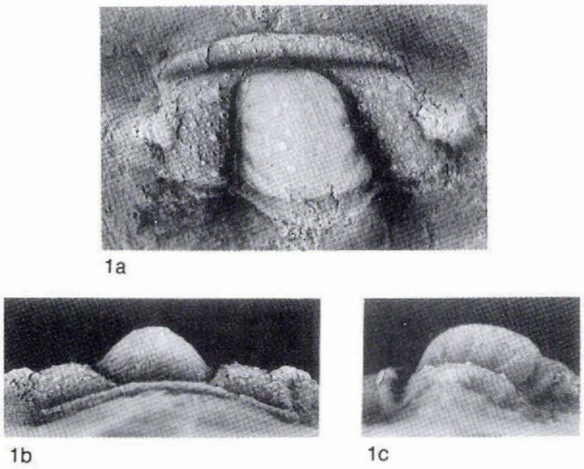


Fig. 23. *Solenopleurella transversa*? Rasetti.
1, partly exfoliated cranidium in dorsal (a), frontal (b), and left-lateral (c) views, MGUH 21.297 from GGU 319790, × 8.

(USNM 145034) reveals the presence of a third pair that is very faintly impressed.

Occurrence. Present in a packstone bed of the basal Kap Stanton Formation at locality 2, Nyeboe Land. It is associated with trilobites indicative of the *Ptychagnostus atavus* Zone of Robison (1984). The holotype is from the Pleasant Hill Limestone (upper Middle Cambrian) of Henrietta, Blair County, Pennsylvania (Rasetti, 1965).

Family Zacanthoididae Swinnerton

Genus *Zacanthoides* Walcott, 1888

Embolimus Rominger, 1887, p. 15; Woodward, 1902, p. 539

Zacanthoides Walcott, 1888, p. 165; Miller, 1889, p. 569; Beecher, 1897, p. 191; Matthew, 1897, p. 187; Matthew, 1899, p. 63; Lindström, 1901, p. 16; Grönwall, 1902, p. 129; Grabau & Shimer, 1910, p. 273; Kobayashi, 1935, p. 123; Shimer & Shrock, 1944, p. 619; Palmer, 1954, pp. 69, 70; Rasetti *in* Harrington *et al.*, 1959b, p. O227; Suvorova & Pokrovskaia *in* Chernysheva, 1960, p. 77; Palmer, 1968, p. B50; Palmer & Halley, 1979, pp. 96, 97; Young & Ludvigsen, 1989, pp. 20, 21

Type species. Embolimus spinosa Rominger, 1887, p. 15 (= *Zacanthoides romingeri* Resser, 1942, pp. 56, 57).

Remarks. The generic diagnosis of Palmer (1954, p. 69) is followed here.

Zacanthoides sp.

Fig. 24

Material. Six cranidia and three pygidia in GGU 298970.

Remarks. Broken cranidia and pygidia in GGU 298970 belong to a distinctive species of *Zacanthoides*. The cranidium is subtrapezoidal in outline, gently convex, and the anterior margin is slightly curved. It has a low, long glabella that expands slightly forward and is bluntly rounded anteriorly. The axial furrow is weak. Three pairs of large muscle scars are present on the glabella; S1 is long and oblique backwards, S2 is short and transverse, and S3 is oblique forwards. The occipital furrow is shallow, but deepest at the sides. A small median node is present on the occipital ring. The frontal area is approximately one-tenth the total length of the cranidium. The fixigena is flat, and its width is subequal with that of the occipital ring. The palpebral area is long, extending to the anterior end of the occipital ring. The anterior end of the palpebral lobe is continuous with the eye ridge. A well-defined palpebral furrow is present. The course of the anterior section of the facial suture is strongly divergent forward from the palpebral lobe. The posterior limb is not preserved in any specimen. The surface is smooth.

The pygidium, exclusive of the border spines, is semi-elliptical in outline. Its sagittal length is about 0.6 times the width. The axis is convex, and slightly tapered posteriorly. It contains four rings and a long terminal piece. The pleural field is convex, subtriangular, and slightly narrower than the axis. Three pleural furrows are present; the anterior two are distinct and the third is weak. The border is poorly defined, flat, and narrower than the pleural field. Four pairs of marginal spines are present, the anterior two being long, and the posterior two being short. The surface is smooth.

Although seemingly distinctive, the new material of *Zacanthoides* is not assigned to a species because it is not well preserved. It is most similar to *Z. variacantha* Palmer & Halley (1979, p. 97) from the western United States in overall appearance. It differs from that species, however, primarily in having a straighter anterior cranidial border, in lacking a cranidial plectrum, and in having two pairs of elongated marginal pygidial spines instead of one pair.

Occurrence. Present in a packstone bed from approximately 56 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. It is associated with trilobites indicative of the *Ptychagnostus gibbus* Interval-zone of Robison (1984).

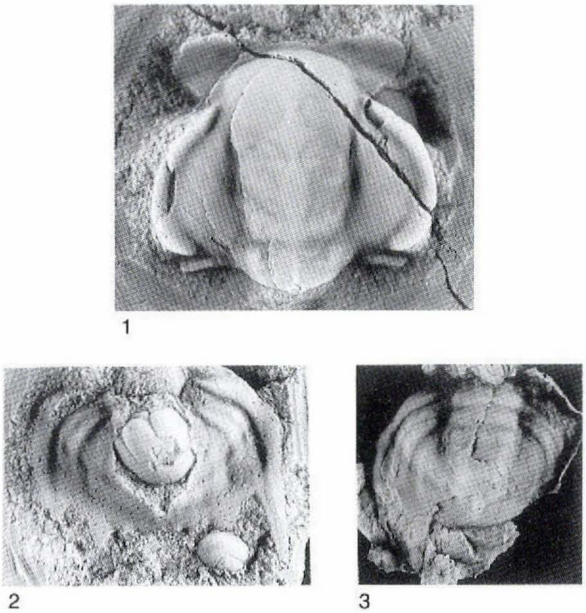


Fig. 24. *Zacanthoides* sp. All specimens from GGU 298970. 1, incomplete cranidium, MGUH 21.298, × 5. 2, incomplete, exfoliated pygidium, MGUH 21.299, × 4. 3, latex cast of incomplete pygidium, MGUH 21.300, × 2.

Family unassigned

Genus *Elrathia* Walcott, 1924

Elrathia Walcott, 1924, p. 56; Robison, 1964, pp. 540, 541 (see for synonymy to 1964); Robison, 1988, p. 92

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

Remarks. The generic diagnosis of Robison (1964) is followed here.

Elrathia sp.

Fig. 25

Material. Several small cranidia and two pygidia in GGU 298970.

Remarks. Several incomplete cranidia and two exfoliated pygidia of a species of *Elrathia* are present in GGU 298970. They are not assigned to species because the material is not well preserved. The cranidium is characterised by having a moderately upturned anterior border, a moderately wide axis, three incipient lateral glabellar furrows, slightly convergent sides of the glabella, a weak medial node on the occipital ring, palpebral lobes that are about one-third the length of the glabella, and moderately strong eye ridges. Fine granules cover the entire cranidium except in the furrows, and faint type 4 caeca radiate from the anterior and anterolateral areas of the axial furrow into the preglabellar field. The pygidium is alate with weak posterolateral swellings. The axis is moderately convex and slightly tapered. It contains four rings, a terminal piece, and a short postaxial ridge. Three pairs of strong furrows are in the pleural lobes.

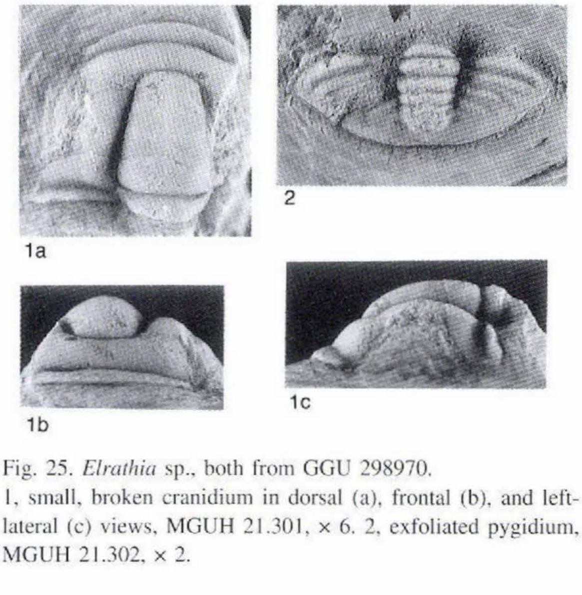


Fig. 25. *Elrathia* sp., both from GGU 298970.
1, small, broken cranidium in dorsal (a), frontal (b), and left-lateral (c) views, MGUH 21.301, × 6. 2, exfoliated pygidium, MGUH 21.302, × 2.

Occurrence. Sclerites are present in wackestone beds approximately 56 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. They are associated with trilobites indicative of the *Ptychagnostus gibbus* Interval-zone of Robison (1984).

Genus *Syspacephalus* Resser, 1936

Syspacephalus Resser, 1936, p. 28; Lochman, 1947, pp. 62–65; Rasetti, 1951, pp. 241, 242; Rasetti, 1955, p. 6; Rasetti *in* Harrington *et al.*, 1959b, p. O237; Suvorova *in* Chernysheva, 1960, p. 117; Shaw, 1962, p. 337; Fritz, 1972, p. 47; Robison, 1976, p. 102; Palmer & Halley, 1979, p. 115

Elrathina Resser, 1937b, p. 11; Diess, 1939, pp. 87, 88; Shimer & Shrock, 1944, p. 611; Rasetti, 1951, p. 221; Howell *in* Harrington *et al.*, 1959b, p. O240; Balashova *et al. in* Chernysheva, 1960, p. 105; Zhuravleva *et al.*, 1970, p. 37; Palmer & Halley, 1979, p. 103; Young & Ludvigsen, 1989, p. 24

Type species. *Agraulos charops* Walcott, 1917, p. 72, by original designation (Resser, 1936, p. 28).

Remarks. Based on the examination of a large number of specimens at the University of Kansas and in the U.S. National Museum, I agree with the conclusion that *Syspacephalus* and *Elrathina* represent a single lineage of trilobites (Robison, 1976, p. 102). Representatives of this ptychopariid lineage show considerable morphological variation in the cranidium, and, although individual species may appear distinct, evaluation of all species assigned to both genera indicates that there are no consistent and meaningful differences between *Syspacephalus* and *Elrathina*.

Syspacephalus sp. 1

Figs 26.1–4

Material. Six cranidia and three librigenae in GGU 298969.

Remarks. Isolated cranidia in GGU 298969 represent a species of *Syspacephalus* that has a narrow glabella, long and shallow lateral glabellar furrows, a convergent and convex anterior branch of the facial suture, and a weak eye ridge. Associated librigenae are characterised by being narrow and having a long genal spine.

Occurrence. Disarticulated sclerites are present in a packstone bed from approximately 71 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. The specimens are from the *P. atavus* Interval-zone.

Syspacephalus sp. 2

Figs 26.5, 6; 31.4a

Material. Numerous cranidia in GGU 298970.

Remarks. This species of *Syspacephalus* is characterised by a moderately long, smooth cranidium. The glabella is almost parallel-sided, narrow, slightly rounded anteriorly, and slightly but distinctly notched at the fossula, especially in small holaspides. The lateral furrows are deep in small holaspides, and shallow to moderately deep in large holaspides; S1 are geniculate, S2 are straight and weakly oblique backward, and S3 are transverse with a distinct anteromedial depression. The occipital furrow is deep

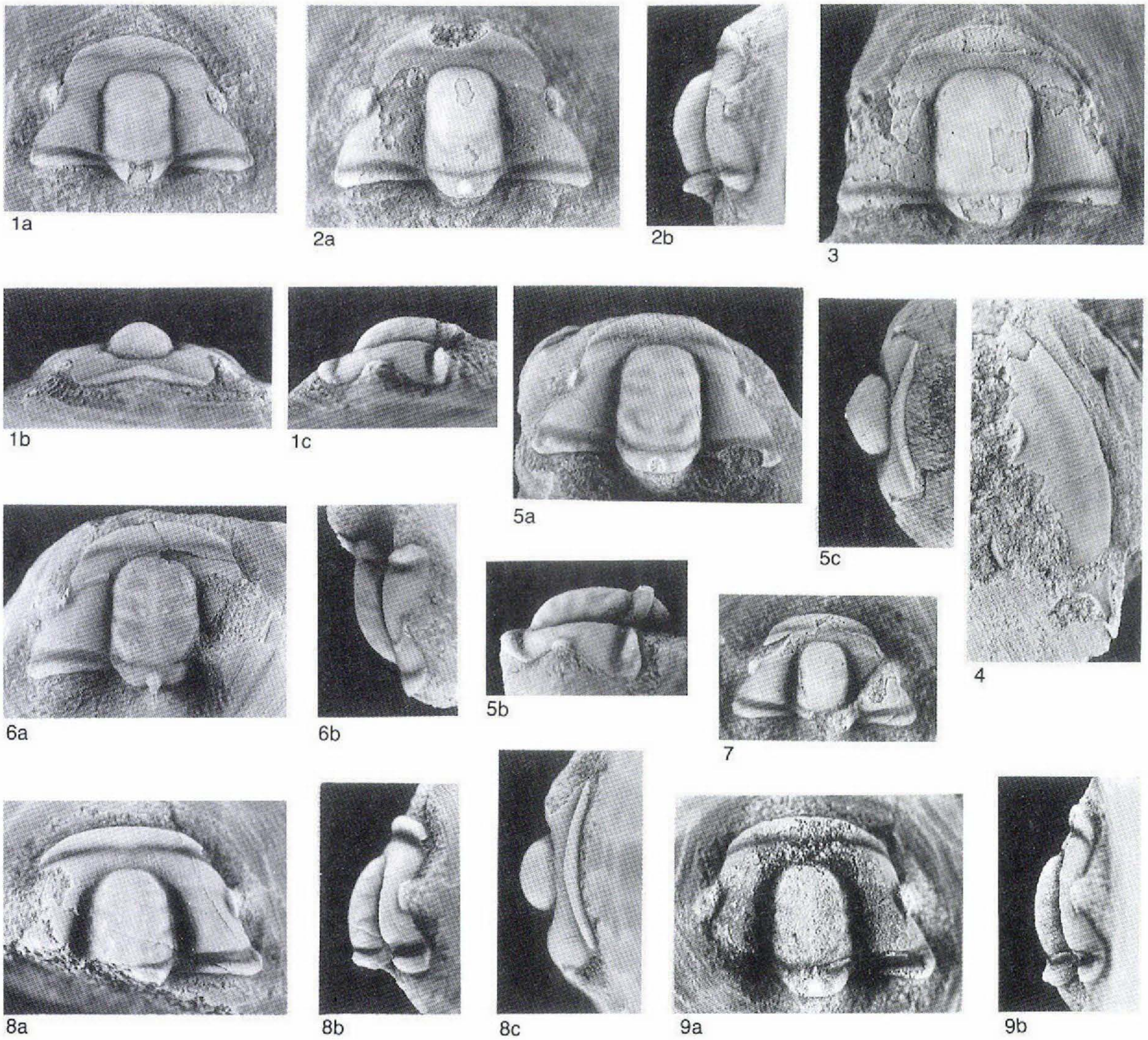


Fig. 26. Specimens of *Syspacephalus*.

1–4, *Syspacephalus* sp. 1, all from GGU 298969. 1, cranidium in dorsal (a), frontal (b), and left-lateral (c) views, MGUH 21.304, × 6. 2, cranidium in dorsal (a) and right-lateral (b) views, MGUH 21.305, × 6. 3, cranidium, MGUH 21.306, × 6. 4, incomplete librigena, MGUH 21.307, × 6.

5–6, *Syspacephalus* sp. 2, both from GGU 298970. 5, cranidium in dorsal (a), left-lateral (b), and frontal (c) views, MGUH 21.309, × 3. 6, cranidium in dorsal (a) and left-lateral (b) views, MGUH 21.308, × 3; occipital spine was probably broken and healed during life.

7–9, *Syspacephalus* sp. 3. 7, small cranidium, MGUH 21.310 from GGU 298972, × 7. 8, broken cranidium in dorsal (a), right-lateral (b), and frontal (c) views, MGUH 21.311 from GGU 298971, × 6. 9, weathered, exfoliated cranidium in dorsal (a) and right-lateral (b) views, MGUH 21.312 from GGU 298971, × 6.

abaxially and shallows medially; the occipital ring is moderately large and has a moderately long, slender, hook-like medial spine projecting vertically then backward. The frontal area is relatively short, and the anterior border is wider than the preglabellar field. Anteriorly, the fixigena is relatively narrow, and posteriorly it is wide. The anterior border furrow is shallow and wide, and the posterior border furrow is deep and wide. Eye ridges are usually strong.

Occurrence. Cranidia are abundant in a packstone bed from approximately 56 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. They are associated with eodiscids and agnostoids indicative of the *Ptychagnostus gibbus* Interval-zone of Robison (1984).

Syspacephalus sp. 3

Fig. 26.7–9

Material. Five cranidia in GGU 298971 and 298972.

Remarks. Broken cranidia in GGU 298971 and 298972 resemble specimens of *S. spinifera* Rasetti, 1951, from British Columbia. The major observed difference between specimens is that those from North Greenland have a slightly longer frontal area of the cranidium than do those from British Columbia.

Occurrence. Present in wackestone beds of the Henson Gletscher Formation at locality 1, Nyeboe Land. Associated polymeroid trilobites indicate a correlation with the *Glossopleura* Zone of the Laurentian shelf.

'Polymerida' *incertae sedis*: 'Eodiscidae'

Remarks. Conclusions about the phylogenetic relationships of eodiscid trilobites have differed for more than a century because, as a group, they include characters common to both polymeroids and agnostoids. Kobayashi (1943a, 1943b, 1944) reviewed early interpretations of the relationships and evolution of eodiscids. More recently, they have been considered to be agnostoids (e.g., Howell *in* Harrington *et al.*, 1959b), ancestors of agnostoids (e.g., Jell, 1975), similar to ancestors of agnostoids (Müller & Walossek, 1987), and of doubtful assignment (Robison, 1987).

To further evaluate eodiscid relationships, I included six genera of eodiscids in a cladistic analysis with six genera of polymeroids, two condylopygids, three agnostoids, and one nektaspid. The taxa selected represent nine major groups of trilobites present in Lower or Middle Cambrian rocks. The groups are olenellids (represented by *Olenellus*), redlichiids (represented by *Xystridura*), ptychopariids (represented by *Elrathia*), corynexochids (represented by *Olenoides*), oryctocephalids (represented by *Tonkinella* and *Thoracocare*), eodiscids (represented by *Eodiscus*, *Dawsonia*, *Costadiscus*, *Pagetia*, *Pagetides*, and *Neocobboldia*), condylopygids (represented by *Condylopyge* and *Pleuroctenium*), agnostoids (represented by *Agnostus*, *Peronopsis*, and *Ptychagnostus*), and nektaspids (represented by *Naraoia*). For consistency in evaluating all the taxa, 22 characters of adult, dorsal morphology were used (Table 3). Characters of juvenile or ventral morphology, which have been shown to be of importance in analyzing phylogenetic relationships among many trilobites (Fortey, 1990), were not used because they are incompletely known in many of the analyzed taxa. Results on 'polymeroid' taxa using this technique are in general agreement with results obtained previously that incorporated data on the dorsal and ventral morphology of the exoskeleton (Fortey, 1990).

The trilobites were analyzed cladistically using the PAUP (Phylogenetic Analysis Using Parsimony) program (Swofford, 1989). To avoid incorporating *a priori* assumptions about the significance of different characters in determining affinity, all characters were equally weighted. Transformation states were polarised using the outgroup method. The data set was analyzed using a hypothetical outgroup based on merostomes and crustaceans because identifying the most primitive group of trilobite is contentious (Babcock, 1990b).

Five parsimony trees were discovered, but only the majority-rule consensus tree has been illustrated (Fig. 27). The Agnostida evidently comprises a highly derived, monophyletic group (or clade) from which the eodiscids, condylopygids, and *Naraoia* are excluded. This interpretation differs from that of Briggs & Fortey (1989) in which *Naraoia* and the agnostoids are interpreted as having fewer derived characters than polymeroids. Synapomorphies (shared derived characters) of the agnostoids are a saddle-like labrum, basal lobes on the cephalon, an edge-to-edge cephalothoracic hinge, two segments in the anteroaxis of the pygidium, and highly modified tips on the thoracic segments. The condylopygids also seem to form a clade, being united by the shared derivation of median nodes or ridges on all thoracic segments and an expanded posteroaxis of the pygidium. Lack of a calcified exoskeleton in *Naraoia* must be interpreted as a secondary loss of a character rather than a symplesiomorphic condition.

Trilobites collectively classified in the order Polymerida (e.g., Robison, 1987), including eodiscids, are apparently not united by synapomorphic characters. Dorsal ecdysial sutures, eye ridges, and articulating half-rings, which were previously interpreted to be synapomorphies

Table 3. Characters used to express relationships among eodiscid and other trilobites

Characters and character states used to construct the cladogram (Fig. 27) expressing inferred relationships among eodiscid and other trilobites. Character states are those of holaspid specimens. Generalized primitive characters of crustaceans and merostomes have been used to create a hypothetical outgroup for the purpose of polarizing character transformations. A question mark indicates missing data.

1. Maximum exoskeletal length: greater than 1 cm (0); less than 1 cm (1).
2. Cephalic sutures: marginal (0); circum-ocular (1); absent (2).
3. Number of thoracic segments: greater than 5 (0); 3 to 5 (1); 2 (2); 0 (3).
4. Shape of labrum: plate-like (0); saddle-like (1).
5. Pleural region of pygidium: segmented (0); effaced (1).
6. Eyes: present, centrally located (0); present, nearly marginal (1); absent (2).
7. Basal lobes: absent (0); present (1).
8. Glabella: short, tapered (0); long, anteriorly expanded (1); short, anteriorly expanded (2); long, tapered (3); long, bulbous anteriorly (4).
9. Cephalothoracic hinge: overlapping (0); edge-to-edge (1).
10. Glabellar segmentation: 3 to 4 lateral furrows (0); single transglabellar furrow (1).
11. Segmentation in pygidial axis: fully segmented (0); 3 segments in anteroaxis (1); 2 segments in anteroaxis (2).
12. Median node or ridge on anteroaxis of pygidium: without node or ridge (0); with node (1); with ridge (2).
13. Pleural tips of last thoracic segment: posteriorly directed (0); anteriorly directed (1).
14. Median node or ridges on all thoracic segments: absent (0); present (1).
15. Posteroglabella: without node or ridge (0); with node (1); with ridge (2).
16. Axis of pygidium: tapered (0); expanded posteriorly (1).
17. Eye ridges: present (0); absent (1).
18. Axial width relative to pleurae: narrow (0); wide (1).
19. Calcification of exoskeleton: absent (0); present (1).
20. Terrace lines on border: present (0); absent (1).
21. Genal spines: present, short to intermediate length (0); present, long (1); absent (2); secondary (3).
22. Borders: not ridge-like (0); ridge-like on cephalon (1); ridge-like on cephalon and pygidium (2).
23. Pygidium: 3 or fewer unreleased segments (0); 4 or more unreleased segments (1); secondarily reduced (2).
24. Preglabellar furrow: absent (0); present (1).
25. Metafixigenal spine: absent (0); present (1).
26. Palpebral lobes: short to intermediate length (0); long (1); absent (2).

Genera	Characters					
		1	11111	11112	22222	2
	12345	67890	12345	67890	12345	6
Outgroup	00000	00000	00000	00000	00000	0
Naraoia	023?1	20300	00000	01001	20200	2
Olenellus	00000	00400	00000	00010	00000	0
Xystridura	01000	00400	00000	00010	00101	1
Elrathia	01000	00000	00000	00010	00100	0
Olenoides	01000	00100	00000	00010	00100	0
Thoracocare	11210	10100	00000	00111	12100	0
Tonkinella	01110	10100	00000	00011	11100	0
Costadiscus	12100	20000	00000	00011	22100	2
Pagetides	11100	10000	00000	00011	22100	0
Eodiscus	12100	20000	00000	01011	22100	2
Pagetia	11200	10000	00000	00011	22100	0
Serrodiscus	12101	20000	00000	01011	32100	2
Dawsonia	12200	20000	00000	01011	22100	2
Neocobboldia	11100	10000	00000	01011	21200	0
Peronopsis	12211	21011	21101	01111	22200	2
Ptychagnostus	12211	21011	21101	01111	22210	2
Agnostus	12211	21011	20101	01111	22210	2
Condylopyge	122?0	202?0	12012	11110	22200	2
Pleuroctenium	122?0	202?0	12012	1111?	32200	2

of polymeroids (Briggs & Fortey, 1989), are here interpreted as symplesiomorphies of polymeroids, agnostoids, and condylopygids. The absence of these character states in agnostoids and condylopygids is probably due to reduction related to paedomorphosis. On the best available evidence from adult morphology, the 'Polymerida' seems to be paraphyletic. A paraphyletic group is a grade or ancestral taxon. It contains some but not all of the descendants of a common ancestor. Membership in the group is defined only by the absence of more derived descendants. For convenience, I have continued use of the term 'Polymerida' elsewhere in this paper, even though the taxon seems to be artificial in a phylogenetic sense.

The eodiscid genera seem to be polyphyletic from trilobites of the order Polymerida. Synapomorphous characters have not yet been identified for eodiscids. Rather, these trilobites seem to be characterised by an extreme reduction of some characters common in other polymeroids. Some such characters as the labrum, however, seem to be relatively unmodified from the polymeroid condition (see Jell, 1970; Zhang, 1989). Reduction is inferred to have taken place primarily through paedomorphosis (probably progenesis in most examples). Analogous patterns of reduction have been inferred in the evolution of *Thoracocare* (Robison & Campbell, 1974) and *Tonkinella* (McNamara, 1986b), both from oryctocephalid ancestors. On account of the variety of combinations of characters that have been reduced (including eyes, facial sutures, number of thoracic segments, and segmentation in the pleural region of the axis), it is inferred that some expressions of reduction have occurred

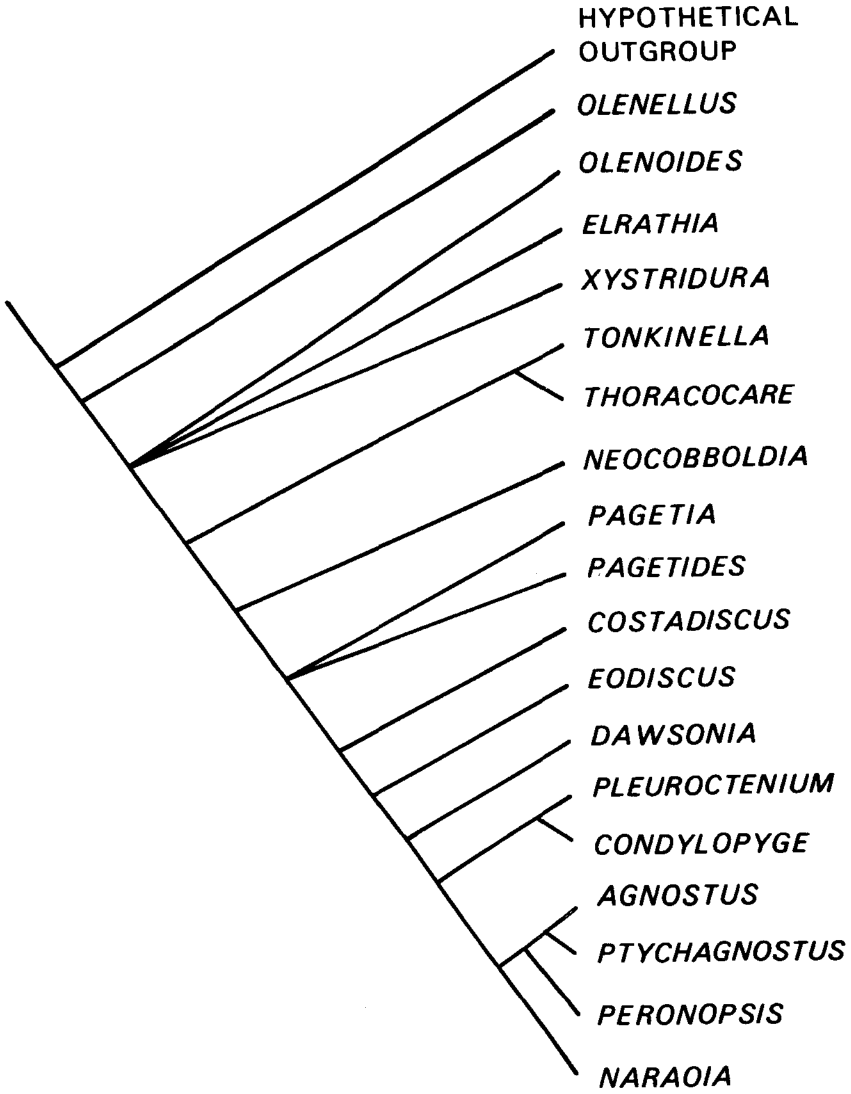


Fig. 27. Majority-rule cladogram illustrating hypothesized phylogenetic relationships among selected trilobite genera, based on characters preserved in holaspides. The outgroup is hypothetical, and based on symplesiomorphic arthropod characters expressed in crustaceans and merostomes.

independently in more than one lineage. Jell (1975, 1990), for example, provided cogent arguments for considering blindness to have been achieved independently in at least three eodiscid lineages. The eodiscid condition, therefore, probably represents a grade of evolution in trilobites rather than a clade. Available evidence does not suggest that agnostoids and eodiscids shared a close common ancestor.

In consideration of the uncertain phylogenetic status of the eodicids, I consider all eodiscid genera to be *incertae sedis* with respect to other polymeroids. This convention follows that discussed by Wiley (1979) for artificial taxa.

Genus *Eodiscus* Hartt *in* Walcott, 1884

Type species. *Eodiscus pulchellus* Hartt *in* Walcott, 1884, p. 24 (by monotypy). *E. pulchellus* is a subjective junior synonym of *Microdiscus scanicus* Linnarsson, 1883, p. 29 (see Rasetti, 1952, pp. 439, 447).

Remarks. Rasetti (1952, p. 447) discussed the generic concept of *Eodiscus*, and synonymous generic names. His concept of the genus is followed here.

Eodiscus scanicus (Linnarsson, 1883)

Figs 9.2a, 28

Microdiscus scanicus Linnarsson, 1883, p. 29, pl. 4, figs 17, 18; Grönwall, 1902, p. 79

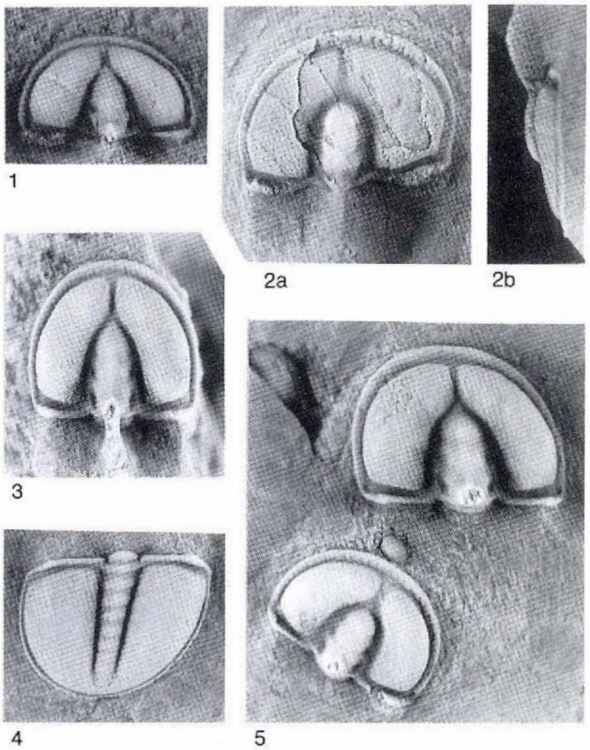


Fig. 28. *Eodiscus scanicus* (Linnarsson). All specimens from GGU 319790, unless otherwise stated.
1, small cephalon, MGUH 21.313, × 10. 2, partly exfoliated cephalon with occipital ring in dorsal (a) and left-lateral (b) views, MGUH 21.314 from GGU 298969, × 7. 3, partly exfoliated cephalon, MGUH 21.315, × 7. 4, pygidium, MGUH 21.316, × 7. 5, two cephala, MGUH 21.317 (above) and MGUH 21.318 (below), × 7.

Microdiscus punctatus Salter. Whiteaves, 1878, p. 225; Walcott, 1884, p. 24, pl. 2, fig. 1; Lesley, 1889, p. 405, fig. 1; Lake (in part), 1907, p. 36; Nicholas (in part), 1916, p. 460

Eodiscus pulchellus Hartt *in* Walcott, 1884, p. 24; Grabau & Shimer, 1910, p. 248, fig. 1543, h, i; Raymond, 1913, p. 103, fig. 2; Kobayashi, 1943a, p. 39; Kobayashi, 1944, pp. 52, 53, 56–58

Microdiscus punctatus var. *pulchellus* Hartt. Matthew, 1886, p. 74, pl. 7, fig. 12

Microdiscus punctatus var. *precursor* Matthew, 1886, p. 75, pl. 7, fig. 13

Microdiscus precursor Matthew. Matthew, 1896, p. 239, pl. 17, fig. 7, text-fig

Microdiscus pulchellus (Hartt). Matthew, 1896, p. 242, pl. 17, fig. 8

Eodiscus scanicus (Linnarsson). Raymond, 1913, p. 104, fig. 10; Yanishevski, 1950, pl. 1, figs 10–14; Rasetti, 1952, pp. 447, 448, pl. 53, figs 7–16, pl. 54, figs 10–16; Hutchinson, 1962, p. 59, pl. 2, figs 1, 2; Rushton, 1974, p. 89; Morris, 1988, p. 91; Robison, 1994, fig. 27.1 (left)

Eodiscus praecursor (Matthew). Raymond, 1913, p. 103, fig. 8

Microdiscus punctatus var. *scanicus* Linnarsson. Illing, 1916, p. 423, pl. 33, figs 11, 12

?*Microdiscus* cf. *M. punctatus* Salter. Strand, 1929, p. 348

Spinodiscus punctatus scanicus (Linnarsson). Kobayashi, 1943a, p. 39; Kobayashi, 1944, p. 57

Spinodiscus matthewi Kobayashi, 1943a, p. 39; Kobayashi, 1944, pp. 56–58

Deltadiscus praecursor Kobayashi, 1943a, p. 39; Kobayashi, 1944, p. 60, pl. 1, fig. 10 (also printed as *Deltacandus*)

Dawsonia canadensis Kobayashi, 1944, p. 60, pl. 2, fig. 14

Eodiscus punctatus scanicus (Linnarsson). Westergård, 1946, pp. 24–26, pl. 1, figs 6–11

Lectotype. Cephalon (selected from Linnarsson's syntypes) by Westergård, 1946, p. 26), SGU Type 5602.

New material. Numerous sclerites in GGU 298969, 298974, 319789, and 319790.

Remarks. This species was adequately diagnosed by Westergård (1946, pp. 24–26), who regarded it as a subspecies of *Eodiscus punctatus* (Salter, 1864) because intermediates are recognised between it and *E. punctatus*. I follow Rasetti (1952) and Hutchinson (1962) in assigning this taxon species rank because of significant differences in the stratigraphic ranges of *E. scanicus* and *E. punctatus*, even though their ranges seem to be bridged by morphological intermediates.

Occurrence. Common in packstone approximately 71 to 73 m above the base of the Henson Gletscher Formation at locality 1, and in the basal beds of the Kap Stanton Formation at locality 2. In North Greenland, as in northern and western Europe, *E. scanicus* is associated with trilobites of the *Ptychagnostus atavus* Interval-zone of Robison (1984). *E. scanicus* is widespread in western Europe. Material has been collected from Sweden, Norway, and Great Britain (Westergård, 1946, p. 26). In accreted terranes of eastern North America, *E. scanicus* has been reported from the *Paradoxides hicksii* Zone of eastern Newfoundland (Howell, 1925, as reassigned by Westergård, 1946, p. 26; see also Hutchinson, 1962) and from the *Paradoxides abenacus* Zone of New Brunswick (Rasetti, 1952, p. 448).

Genus *Costadiscus* n. gen.

Etymology. From Latin, *costa*, rib, and *discus*, disk; in reference to the multiribbed pygidium.

Type species. *Costadiscus minutus* n. gen., n. sp.

Diagnosis. Cephalon semicircular, wider than long; glabella narrow, tapered, angular anteriorly; preglabellar field wide; cheeks separated by preglabellar median furrow; border narrow laterally, expanding anteriorly; eyes absent; occipital ring expanded into spine; baccula present; posterior border furrow joins baccular furrow. Holaspid thorax with three segments; segment 1 transversely narrower than segments 2 or 3; pleural tips point backward in segment 1, forward in segments 2 and 3. Pygidium semicircular, wider than long. Axis narrow, not reaching posterior border furrow, having 8 segments. Pleural field having 8 segments, continuous to posteromedial line. Border narrow.

Remarks. Trilobites of this genus are characterised by a narrow axis, a glabella that is angular anteriorly, a lack of eyes and facial sutures, a border furrow that joins the baccular furrows, three thoracic segments in the holaspid period, a wide border on the anterior cephalon, a narrow border on the pygidium, and a pygidium having deep furrows in the pleural field and eight pleural segments.

The cephalon of *Costadiscus* n. gen. is most similar to that of *Eodiscus* Hartt *in* Walcott, 1884, but the pygidium resembles that of *Dawsonia* Hartt *in* Dawson, 1868. If sclerites are found separately, they could easily be confused with *Eodiscus* or *Dawsonia*. The cephalon of *Costadiscus* differs from *Eodiscus* primarily in the glabella, which is angular anteriorly, and in the posterior border furrow, which joins the baccular furrow. The pygidium of *Costadiscus* differs from *Dawsonia* in having one or two more axial rings, three more segments in the pleural field, and a much narrower border.

At present, only the type species, *C. minutus* n. sp., is included in *Costadiscus*.

Costadiscus minutus n. sp.

Fig. 29

Etymology. From Latin, *minutus*, little or small; in reference to the small exoskeleton of this species.

Holotype. Nearly complete specimen, MGUH 21.322.

Material. Four nearly complete specimens, and 15 disarticulated specimens in GGU 298969, 319789, and 319790.

Diagnosis. As for genus.

Description. Cephalon about 1.4 times wider than long exclusive of occipital ring and spine. Glabella high, reaching greatest width across L1; S1 deep, convex, oblique backward; S2 deep laterally, shallowing medially, simple, straight. Occipital furrow deep at sides, moderately impressed and straight across axis. Occipital spine reaching to third thoracic segment in holaspid; median node of variable expression at base of spine. Cheeks higher than glabella, highest about midway across, rapidly sloping to anterior and lateral border furrow; preglabellar furrow distinct. Baccula low, subtriangular; low ridges connect inner part of baccular furrow to occipital ring. Holaspid genal angle rounded, meraspid genal angle angular. Ridges on anterior and lateral border low, narrow, closely spaced.

Holaspid thorax with three segments, axis moderately high, pleurae flattened. Segment 1 transversely narrower than cephalon, segments 2 and 3 about as wide as cepha-

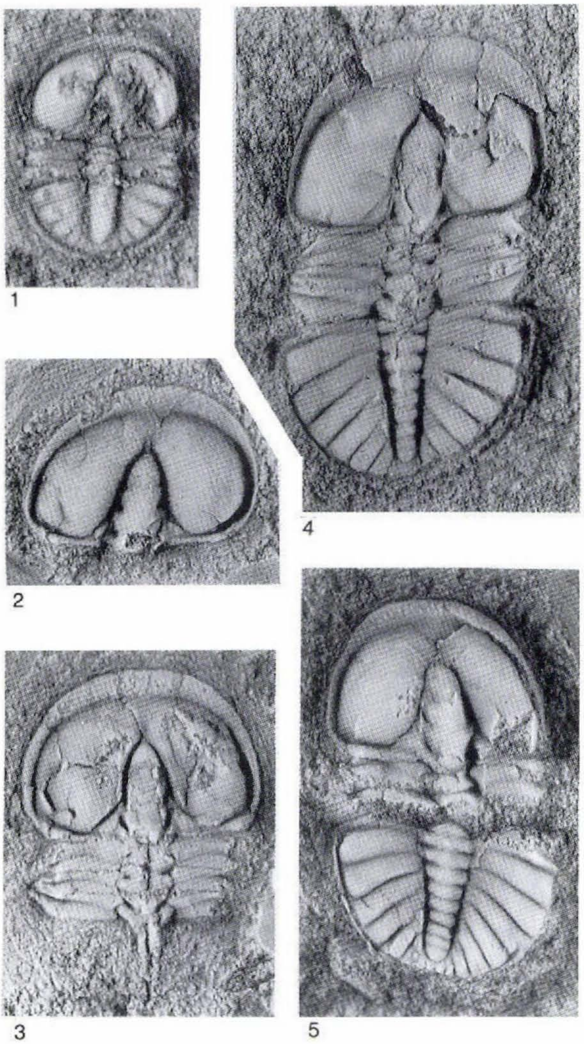


Fig. 29. *Costadiscus minutus* n. gen., n. sp. All specimens from GGU 298969.

1, small exoskeleton, MGUH 21.319, × 8. 2, cephalon, MGUH 21.320, × 7. 3, specimen lacking pygidium but showing spines extending from occipital ring and axis of third segment, MGUH 21.321, × 7. 4, holotype exoskeleton, MGUH 21.322, × 7. 5, specimen lacking third thoracic segment, MGUH 21.323, × 7.

lon. Pleural tip rounded and posterolaterally directed in segment 1, angular and anterolaterally directed in segments 2 and 3. Pleural furrows distinct; in segment 1 strongly concave near axial furrow, strongly convex laterally and distally; in segment 2 moderately concave near axial furrow, nearly straight laterally and distally; in segment 3 strongly concave near axial furrow, moderately convex laterally then turned strongly forward distally. Axis about 1.5 times wider than maximum glabellar width; third axial ring with median spine reaching to about middle of pygidium.

Pygidium about 1.4 times wider than long. Axis narrow, gradually tapering, not reaching posterior border furrow, higher than pleural furrow, having eight segments plus terminal piece; first axial ring with small median node; ring furrows deep, continuous for entire length; axial furrows deep. Pleural field high, highest about midway across, rapidly sloping to border furrow, with eight segments, interpleural furrows deep distally, gradually shallowing medially. Border narrow, anterior border thickened laterally; articulating facets truncating anteropleural corners.

Dorsal surface smooth except for anterior and lateral cephalic border, which is finely granulated.

Ontogeny. Growth stages represented are meraspid degrees 1 and 2, and several holaspid instars. Protaspides have not been recognised in *C. minutus*. Normal size increase in *C. minutus* is accompanied by the following morphological changes during the meraspid and holaspid periods: retraction of the glabella, change in shape of the genal angles from angular to broadly rounded, increase in number of thoracic segments to three, movement of segments forward from the anterior of the pygidium, increase in number of both pygidial axial rings and pygidial pleurae from five in meraspid degree 1 to eight in holaspid period, relative decrease in width of the pygidial border, reduction of relief of both the cephalon and pygidium, and development of granulation on the cephalic border during the holaspid period. The occipital and medial thoracic spines are broken in all studied meraspides, and any changes in these characters are unknown.

Occurrence. Common in mudstone and packstone beds approximately 71 to 73 m above the base of the Henson Gletscher Formation at locality 1 and in the basal beds of the Kap Stanton Formation at locality 2. The species is associated with trilobites indicative of the *Ptychagnostus atavus* Interval-zone of Robison (1984).

Genus *Opsidiscus* Westergård, 1949

Aulacodiscus Westergård, 1946, p. 26; Hupé, 1953, p. 170; not *Aulacodiscus* Douvillé, 1921 (Gastropoda; see Westergård, 1949, p. 606)

Opsidiscus Westergård, 1949, p. 606; Rasetti *in* Harrington *et al.*, 1959b, p. O188; Pokrovskaya, 1959, p. 177; Pokrovskaya *in* Chernysheva, 1960, p. 56; Poletaeva & Romanenko, 1970, p. 73; Jago, 1972b, pp. 227–229; Jell, 1975, pp. 75–78

Type species. *Aulacodiscus bilobatus* Westergård (1946, pp. 26–28), by original designation (Westergård, 1949).

Remarks. The concept and content of this genus were thoroughly reviewed by Jell (1975, pp. 75–78).

Opsidiscus longispinus n. sp.

Fig. 30

Etymology. From Latin, *longus*, long, and *spina*, spine; in reference to the elongate occipital spine.

Holotype. Cephalon, MGUH 21.325.

Material. Three cephala in GGU 319789 and 319790.

Diagnosis. *Opsidiscus* having straight medial margin on cephalon; posterior glabellar part wider and more convex than anterior part, transglabellar furrow distinct; occipital spine long, slender; eye convex, located subcentrally on gena; eye ridge strongly curved, convex near axial furrow, indistinct near palpebral lobe; border furrow without scrobicules.

Description. Cephalon semicircular in outline, anterior margin straight medially, anterolateral corner well-rounded, posterolateral corner geniculate. Glabella bi-

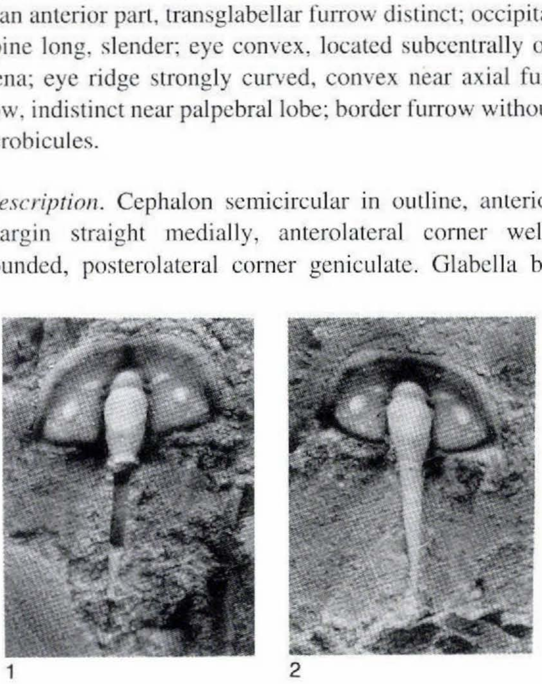


Fig. 30. *Opsidiscus longispinus* n. sp., both from GGU 319790. 1, cephalon with broken occipital spine, MGUH 21.324, × 16. 2, holotype cephalon, MGUH 21.325, × 16.

lobed; anterior part narrow, short, convex, and rounded anteriorly; transglabellar furrow straight; posterior part about 1.5 times length of anterior part, strongly convex, elevated well above gena and anterior part, expanding slightly forward; lateral furrows absent. Occipital spine long, thick, directed away from cephalon at about 10 degree angle; length beyond posterior margin of occipital ring about 1.6 times cephalic length exclusive of spine. Occipital ring subequal in width with widest part of posterior glabella, continuous with occipital spine. Occipital furrow indicated only at sides by distinct pit. Axial furrow moderately deep, moderately wide in front, narrower at side, with distinct pits at intersection with transglabellar furrow. Bacculae absent. Genae convex, sloping at sides, moderately sloping at front, separated by shallow preglabellar median furrow. Eye convex, moderately long, wide, slightly crescentic; located subcentrally on gena. Eye ridge originates in axial furrow about one-third distance from back of anterior part of glabella, forms narrowly curved arc to anterior end of palpebral lobe; adaxial one-half of length convex, abaxial one-half indistinct. Facial suture absent. Preglabellar field subequal in length with anterior part of glabella. Border furrow shallow, moderately wide in front, narrowing and slightly deepening laterally, narrow and deep posteriorly; pits absent. Border narrow, slightly convex anteriorly and laterally; slightly narrowed at posterolateral corner, upturned at genal angle, rapidly narrowing toward occipital ring. Surface of cephalon smooth or with several small granules on cheek behind eye.

Thorax and pygidium unknown.

Remarks. In characters of the cephalon, *O. longispinus* differs from all described species of the genus by having a distinctly bipartite glabella with a posterior part that is markedly wider and more convex than the anterior part, by having a convex eye that is located near the middle of the gena, and by having a strongly arcuate eye ridge. Aside from *O. longispinus*, complete occipital spines are known from *O. altaicus* Poletaeva *in* Poletaeva & Romanenko (1970), *O. antarcticus* (Palmer & Gatehouse, 1972), *O. brevicaudatus* Jell (1975), *O. depolitus* Romanenko *in* Poletaeva & Romanenko (1970), *O. microspinus* Jell (1975), and *O. teretistes* Jell (1975). Among these species, the spine of *O. longispinus* is by far the longest. It is also evenly tapered, unlike that in *O. altaicus*, *O. brevicaudatus*, and *O. teretistes*. Besides *O. longispinus*, only *O. antarcticus* and some specimens of *O. argusi* Jago (1972b) lack scrobicules in the border furrow. The presence of granules over the surface of the cephala of *O. argusi* and *O. bilobatus* (Westergård, 1946), and the presence of functional facial sutures in *O. antarcticus*, further distinguish these species from *O. longispinus*.

Occurrence. Present in a packstone bed of the basal Kap Stanton Formation at locality 2. It is associated with trilobites indicative of the *Ptychagnostus atavus* Interval-zone of Robison (1984).

Undetermined corynexochoid
Fig. 31.1

Remarks. A single, incomplete, exfoliated cranidium, possibly belonging to *Olenoides*, is present in GGU 298970. The specimen is small. Its glabella is parallel-sided, moderately convex, and elevated slightly above the fixigena. It extends well beyond the anterolateral corner of the cranidium and is unfurrowed. The occipital furrow is distinct and a deep pit is developed at the side. The occipital ring has a long, stout medial spine. The fixigena is narrow anteriorly and very wide behind the palpebral lobe. The axial furrow is distinct, and an eye ridge is not evident.

It is possible that this specimen is a small individual of *Olenoides* sp., described above from GGU collection 298970. The present lack of specimens intermediate in size between this specimen and a specimen of *Olenoides* sp. (Fig. 14.1), however, leave some reason for doubt.

Occurrence. Present in a wackestone bed approximately 56 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. It is associated with trilobites indicative of the *Ptychagnostus gibbus* Interval-zone of Robison (1984).

Undetermined ptychoparioid 1
Fig. 31.2

Remarks. Two small, distinctive cranidia are in GGU 298971. They are moderately convex and have a subquadrate glabella with a low, weak, longitudinal ridge medially. Lateral glabellar furrows are moderately deep. The S1 and S2 are geniculate, and the posterior branches are more deeply impressed than the anterior branches. The S3 are straight and slightly oblique forward. The occipital ring is subtriangular and long, being approximately one-third the glabellar length. It extends backward to a sharp point, but does not end in a true spine. A low, weak, longitudinal ridge is present medially. The anterior border is not preserved. The posterior border is convex and narrower than the border furrow. It is backwardly deflected at about midlength. The axial furrow is deep, and weak fossula are present. The fixigenae appear to be narrow although the margins are broken. Strong eye

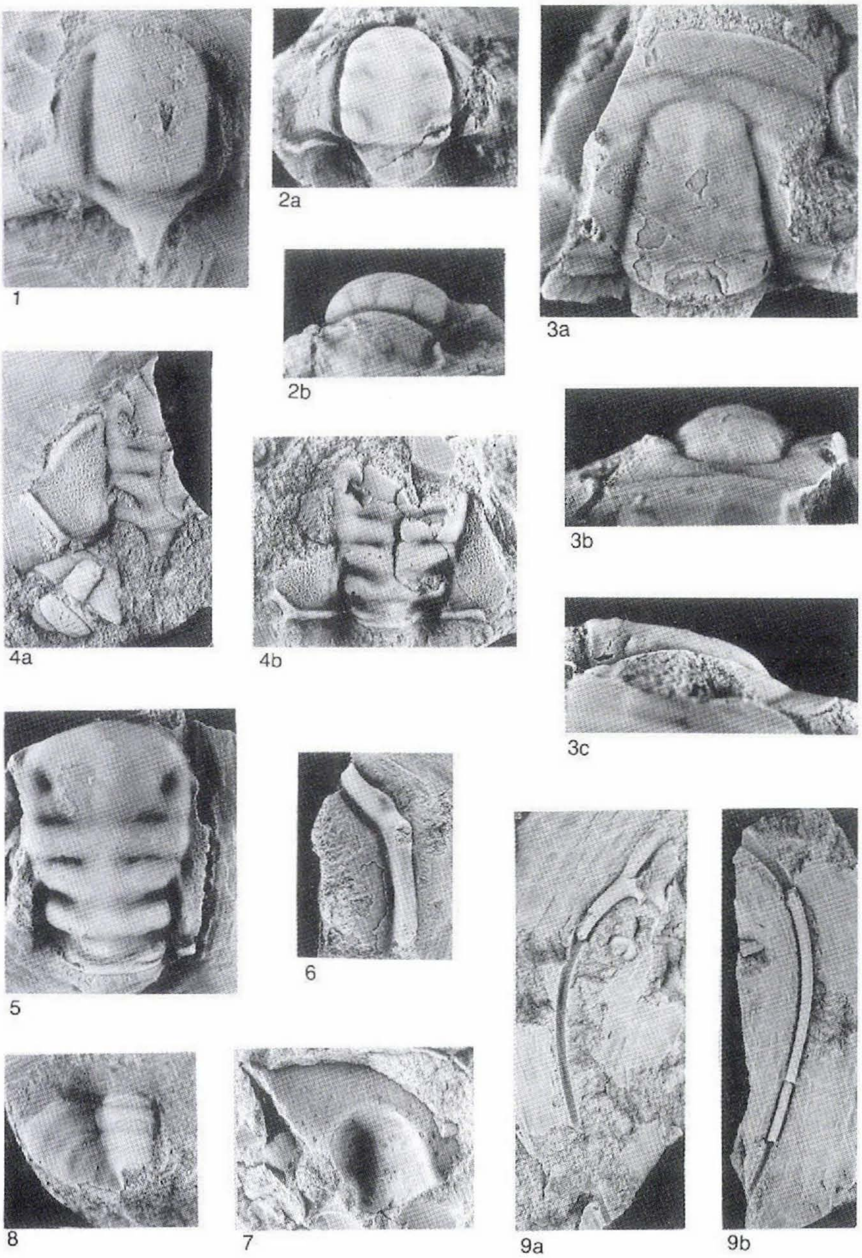


Fig. 31. Undetermined polymeroid trilobites.

1, Undetermined corynexochoid. Incomplete cranidium, MGUH 21.326 from GGU 298970, × 4.5.

2, Undetermined ptychoparioid 1. Incomplete cranidium in dorsal (a) and left-lateral (b) views, MGUH 21.327 from GGU 298971, × 7.

3, Undetermined ptychoparioid 2. Incomplete cranidium in dorsal (a), frontal (b), and right-lateral (c) views, MGUH 21.328 from GGU 298970, × 6.

4–6, Undetermined ptychoparioid 3, all from GGU 298970. 4, incomplete cranidium, latex cast of counterpart (a) and part (b), MGUH 21.329; small cranidium of *Syspacephalus* sp. 2 and cephalon of agnostoid are associated with the counterpart; × 4. 5, axial region of cephalon, MGUH 21.330, × 4. 6, cranidial fragment including part of border, MGUH 21.331, × 4.

7, Undetermined ptychoparioid 4. Incomplete cranidium, MGUH 21.332 from GGU 298970, × 2.

8, Undetermined ptychoparioid 5. Incomplete pygidium, MGUH 21.333 from GGU 298973, × 8.

9, Undetermined ptychoparioid 6. Incomplete librigena with some of the genal spine attached, preserved as part and counterpart (a and b), MGUH 21.334 from GGU 298974, × 1.

ridges, extending strongly obliquely backward from the fossulae, are present.

In general aspect, the cranidium appears to resemble some described species of *Glaphyraspis* and *Welleraspis*. Among preserved characters of the cranidium, however, the new specimens differ from *Welleraspis* and *Glaphyraspis* in lacking a true occipital spine, having geniculate S1 and S2 lateral glabellar furrows, or having a backwardly deflected posterior border. Critical characters of the anterior border and the palpebral lobes are not preserved. The undetermined cranidia are associated with a polymeroid fauna indicative of the *Glossopleura* Zone, and are substantially older than either *Glaphyraspis* or *Welleraspis*.

Occurrence. Present in a wackestone bed approximately 42 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. It is associated with trilobites indicative of the *Glossopleura* Assemblage-zone of Robison (1976).

Undetermined ptychoparioid 2

Fig. 31.3

Remarks. A single fragmentary cranidium in GGU 298970 having some similarities with *Elrathiella* is left in open nomenclature. The specimen is large and relatively low in front and lateral profile. It has a long, slightly tapering glabella that shows four weak pairs of lateral furrows. A weak ridge-like structure extends the length of the glabella. The occipital ring is broken. The occipital furrow is moderately deep at the sides but shallows medially. The axial furrow is moderately deep, and a pair of fossulae is present. Distinct eye ridges are present. The anterior border is wide. The anterior border furrow is shallow and wide, and has a slight backward deflection medially. At its widest, the preglabellar field is about three-quarters the length of the anterior border. Although broken, the anterior parts of the fixigenae were probably wide. The posterior parts of the fixigenae and the palpebral lobes are missing. Type 4 caeca radiate into the preglabellar field.

Occurrence. Present in a packstone bed approximately 56 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. It is associated with trilobites indicative of the *Ptychagnostus gibbus* Interval-zone of Robison (1984).

Undetermined ptychoparioid 3

Figs 31.4–31.6

Remarks. Several broken cranidia of a distinctive polymeroid are present in GGU 298970. The glabella is convex, expanded forward, and contains four deep lateral furrows; S1 is confluent, straight, slightly oblique backwards, and deepest at the sides; S2 and S3 are straight, transverse, and deepest near mid-course; S4 is backwardly directed and pit-like. The occipital ring is exceptionally narrow, and the occipital furrow is unusually wide and deep. The axial furrow is narrow. Little is known of the rest of the cranidium. It is evidently flat, possessing a rather long palpebral lobe, and has a rather narrow upturned border. A putative metafixigenal spine is present at each posterolateral corner. A network of fine raised lines covers at least the posterior part of the fixigenae.

In axial characters, this taxon resembles some paradoxidid trilobites, especially *Centropleura*, *Anopolenus*, and *Clarella*, but none of these taxa has such a short palpebral lobe or occipital ring.

Occurrence. Present in a packstone bed approximately 56 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. It is associated with trilobites indicative of the *Ptychagnostus gibbus* Interval-zone of Robison (1984).

Undetermined ptychoparioid 4

Fig. 31.7

Remarks. Several cranidial fragments in GGU 298970 cannot be assigned to genus. They are characterised by a rather wide border and fixigenae having large, closely spaced granules. The fragments resemble fixigenae of some genera of alokistocarids.

Occurrence. Present in a packstone bed approximately 56 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. It is associated with trilobites indicative of the *Ptychagnostus gibbus* Interval-zone of Robison (1984).

Undetermined ptychoparioid 5

Fig. 31.8

Remarks. A single broken pygidium in GGU 298973 is unassigned. It apparently has a subhemispherical outline, a convex, slightly tapering axis, and a nearly flat pleural area. Three rings and a terminal piece are present in the axis. Three pairs of wide and shallow pleural furrows and two interpleural furrows are present in the pleural region.

Occurrence. Present in a wackestone bed approximately 42 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. It is associated with trilobites indicative of the *Glossopleura* Assemblage-zone of Robison (1976).

Undetermined ptychoparioid 6

Fig. 31.9

Remarks. Several elongate, tubular, and moderately curved genal spines are present in GGU 298974. One specimen has the posterolateral corner of the librigena attached. The genal spines are approximately circular in cross section and smooth externally. Their affinities are unknown although they resemble the genal spines of some Late Cambrian olenid trilobites.

Occurrence. Present in a wackestone bed approximately 73 m above the base of the Henson Gletscher Formation at locality 1, Nyeboe Land. It is associated with trilobites indicative of the *Ptychagnostus atavus* Interval-zone of Robison (1984).

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References

Angelin, N. P. 1851 [dated 1852]: *Palaeontologia Svecica: pars I: iconographia crustaceorum formationis transitionis*. 24 pp. Lund: Weigel.

Angelin, N. P. 1854: *Palaeontologia Scandinavica: pars I: crustacea formationis transitionis*, 21–92. Lund: Weigel.

Angelin, N. P. 1878: *Palaeontologia Scandinavica: pars I: crustacea formationis transitionis.* Fasciculi I & II, 1–24, 21–92. Holmiae (Stockholm): Samson & Wallin.

Archer, A. W. & Maples, C. G. 1987: Monte Carlo simulation of selected binomial similarity coefficients (I): effect of number of variables. *Palaios* **2,** 609–617.

Babcock, L. E. 1990a: *Biogeography, phylogenetics, and systematics of some Middle Cambrian trilobites from open-shelf to basinal lithofacies of North Greenland and Nevada.* Unpublished Ph.D. dissert., Univ. Kansas, 222 pp.

Babcock, L. E. 1990b: Phylogenetic relationships among Cambrian trilobites. *Geol. Soc. Amer. Abstr. Prog.* **22**(7), A265.

Babcock, L. E. 1991: Debris beds containing mixed faunal representatives from shelf-margin biofacies: a tool for use in terrane analysis. *Geol. Soc. Am. Abstr. Prog.* **23**(3), 2.

Babcock, L. E. 1993: Trilobite malformations and the fossil record of behavioral asymmetry. *J. Paleont.* **67,** 217–229.

Babcock, L. E. in press: Arthropoda, class Trilobita. *In* Feldmann, R. M. (ed.) Fossils of Ohio. *Bull. Ohio Dept. Nat. Res., Div. geol. Survey* **70.**

Babcock, L. E. 1994: Biogeography and biofacies patterns of Middle Cambrian polymeroid trilobites from North Greenland: palaeogeographic and palaeo-oceanographic implications. *Bull. Grønlands geol. Unders.* **169** (this volume).

Babcock, L. E. & Robison, R. A. 1989: Paleobiogeographic significance of Middle Cambrian trilobites from North Greenland. *Geol. soc. Am. Abstr. Prog.* **21**(6), A340.

Barrande, J. 1852: *Systeme silurien de centre de la Bohême* **1,** 935 pp. Prague and Paris: published by the author.

Beecher, C. E. 1895: The larval stage of trilobites. *Am. Geol.* **16,** 165–196.

Beecher, C. E. 1897: Outline of a natural classification of the trilobites. *Am. J. Sci.* 4 ser., **3,** 89–106.

Berg-Madsen, V. 1985: The Middle Cambrian of Bornholm, Denmark: a stratigraphical revision of the lower alum shale and associated anthraconites. *Geol. Fören. Stockh. Förhandl.* **106,** 357–376.

Bergström, J. & Levi-Setti, R. 1978: Phenotypic variation in the Middle Cambrian trilobite *Paradoxides davidis* Salter at Manuels, SE Newfoundland. *Geolog. Palaeont.* **12,** 1–40.

Blaker, M. R. 1986: Notes on the trilobite faunas of the Henson Gletscher Formation (Lower and Middle Cambrian) of central North Greenland. *Rapp. Grønlands geol. Unders.* **132,** 65–73.

Blaker, M. R. 1991: Early Cambrian trilobites from North Greenland. Keele Univ. Unpublished Ph.D thesis, 286 pp.

Briggs, D. E. G. & Fortey, R. A. 1989: The early radiation and relationships of the major arthropod groups. *Science* **246,** 241–243.

Brøgger, W. C. 1878: Om paradoxidesskifrene ved Krekling. *Nyt Mag. Naturvid.* **24,** 18–88.

Campbell, L. D. 1971: Occurrence of '*Ogygopsis* shale' fauna in southeastern Pennsylvania. *J. Paleont.* **45,** 437–440.

Chernysheva, N. E. 1953: [Middle Cambrian trilobites from eastern Siberia, part 1]. Moscow: Vses. Nauch.-Issled. geol. Inst. (VSEGEI), 94 pp. [In Russian.]

Chernysheva, N. E. (ed.). 1960: [Principles of paleontology:

arthropods, trilobites and crustaceans]. Moscow: Gosudar. Nauchno-Tekh. Izd. Lit. Geol. Okhr. Nedr., 515 pp. [In Russian.]

Chernysheva, N. E. 1961: [Cambrian stratigraphy of Aldan anticline and paleontological basis of separation of Amginsk Formation]. *Trudy Vses. Nauch.-Issled. geol. Inst.* (VSEGEI) **49,** 278 pp. [In Russian.]

Chernysheva, N. E. 1980: [The genus *Solenopleura* (Trilobita)]. *Paleont. Zhur.* **3,** 65–73. [In Russian.] [English translation: *Paleont. J. (1980),* **3,** 72–80.]

Cobbold, E. S. & Pocock, R. W. 1934: The Cambrian area of Rushton (Shropshire). *Phil. Trans. R. Soc. London* **B 223,** 305–409.

Cooper, G. A. *et al.* 1952: Cambrian stratigraphy and paleontology near Caborca, northwestern Sonora, Mexico. *Smithson. misc. Collns* **119**(1), 184 pp.

Cooper, R. A., Jago, J. B., Laird, M. G., McKinnon, D. I. & Simes, J. E. 1976: Biostratigraphy of Middle and Upper Cambrian faunas from northern Victoria Land, Antarctica. *25 Int. geol. Congr., Sydney, Abstr.* **1,** 300 only.

Cooper, R. A., Jago, J. B., Rowell, A. J. & Braddock, P. 1983: Age and correlation of the Cambrian–Ordovician Bowers Supergroup, northern Victoria Land. *In* Oliver, R. L., James, P. R. & Jago, J. B. (ed.) *Antarctic earth science,* 128–131. Canberra: Australian Acad. Sci.

Czarnocki, J. 1927: Kambri jego fauna w srodkowej czesci Gor Swietokrzyskich. *Bull. Surv. geol. Poland* **4,** 189 only.

Dawes, P. R. 1971: The North Greenland fold belt and environs. *Bull. geol. Soc. Denmark* **20,** 197–239.

Dawes, P. R. 1976: Precambrian to Tertiary of northern Greenland. *In* Escher, A. & Watt, W. S. (ed.) *Geology of Greenland,* 248–303. Copenhagen: Geol. Survey Greenland.

Dawes, P. R. & Soper, N. J. 1973: Pre-Quaternary history of North Greenland. *In* Pitcher, M. G. (ed.) Arctic geology. *Mem. Am. Assoc. petrol. Geol.* **19,** 117–134.

Dawson, J. W. 1868: *Acadian geology. The geological structure, organic remains, and mineral resources of Nova Scotia, New Brunswick, and Prince Edward Island,* 2nd ed., 694 pp. London: MacMillan.

Deiss, C. 1939: Cambrian stratigraphy and trilobites of northwestern Montana. *Spec. Pap. geol. Soc. Am.* **18,** 135 pp.

Demokidov, K. K. & Lazarenko, N. P. 1964: [Stratigraphy of the upper Precambrian and Cambrian and Lower Cambrian trilobites from the northern part of the middle Siberia and islands of Soviet Arctic]. *Trudy Nauchno-Issled. Inst. geol. Arktiki, Gos. geol. Komitet SSSR* **137,** 286 pp. [In Russian.]

Egorova, L. I. *et al.* 1960: *In* Khalfina, L. L. (ed.) [Palaeozoic biostratigraphy of the Sayano-Altay Mountain region]. *Trudy Sib. Nauchno.-Issled. Inst. Geol. Geof. mineral. Syr. (SNIIG-GIMS)* **19,** 497 pp. [In Russian.]

Fletcher, T. P., Higgins, A. K. & Peel, J. S. 1988: A Balto-Scandian Middle Cambrian fauna from Peary Land, North Greenland. *Rapp. Grønlands geol. Unders.* **137,** 118.

Fortey, R. A. 1985: Pelagic trilobites as an example of deducing the life habits of extinct arthropods. *Trans. R. Soc. Edinburgh* **76,** 219–230.

Fortey, R. A. 1990: Ontogeny, hypostome attachment and trilobite classification. *Palaeontology* **33,** 529–576.

Fritz, W. H. 1972: Lower Cambrian trilobites from the Sekwi Formation type section, Mackenzie Mountains, northwestern Canada. *Bull. geol. Surv. Canada* **212,** 90 pp.

Grabau, A. W. & Shimer, H. W. 1910: *North American index fossils,* 853 pp. New York: A. G. Seiler & Co.

Gregory, J. W. 1903: The Heathcotian: a pre-Ordovician series and its distribution. *Proc. R. Soc. Victoria,* n. s., **15**(2).

Grönwall, K. A. 1902: Bornholms Paradoxideslag og deres fauna. *Danm. geol. Unders.* (Ser. 2), **13,** 230 pp.

Gupta, V. J. 1967: Cambrian trilobites from Zachaldor, Baramula district, Kashmir. *Res. Bull. Punjab Univ.* (n. s.) **18,** 275–277.

Harrington, H. J., Moore, R. C. & Stubblefield, C. J. 1959a: Morphological terms applied to Trilobita. *In* Moore, R. C. (ed.) *Treatise on invertebrate paleontology,* part O, *Arthropoda* **1,** O117–O126. Lawrence: Geol. Soc. Am. and Kansas Univ. Press.

Harrington, H. J. *et al.* 1959b: Systematic descriptions. *In* Moore, R. C. (ed.) *Treatise on invertebrate paleontology,* part O, *Arthropoda* **1,** O170–O540. Lawrence: Geol. Soc. Am. and Kansas Univ. Press.

Hawle, I. & Corda, A. J. C. 1847: Prodom einer Monographie der böhemischen Trilobiten. *Abh. K. böhem. Ges. Wiss.* **5,** 176 pp.

Henningsmoen, G. 1957: The trilobite family Olenidae. *Skr. norske Vidensk-Akad.* Mat.-naturv. Kl. 1, 303 pp.

Hicks, H. 1872: On some undescribed fossils from the Menevian Group. *Q. Jl geol. Soc. London* **28,** 173–185.

Higgins, A. K., Friderichsen, J. D. & Soper, N. J. 1981: The North Greenland fold belt between central Johannes V. Jensen Land and eastern Nansen Land. *Rapp. Grønlands geol. Unders.* **106,** 35–45.

Higgins, A. K., Ineson, J. R., Peel, J. S., Surlyk, F. & Sønderholm, M. 1991: Lower Palaeozoic Franklinian Basin of North Greenland. *Bull. Grønlands geol. Unders.* **160,** 71–139.

Hofmann, H. J. & Parsley, R. L. 1966: Antennae of *Ogygopsis. J. Paleont.* **40,** 209–211.

Holm, G. & Westergård, A. H. 1930: A Middle Cambrian fauna from Bennett Island. *Mem. Acad. Sci. l'URSS* **21**(8), 1–25.

Howell, B. F. 1925: The faunas of the Cambrian *Paradoxides* beds at Manuels, Newfoundland. *Bulls Am. Paleont.* **11**(43), 140 pp.

Howell, B. F. 1932: Two new Cambrian trilobites from Vermont. *Bull. Wagner Free Inst. Sci.* **7,** 4–8.

Howell, B. F. 1933: The classification of the trilobite family, Centropleurinae. *Meddr Dansk Geol. Foren.* **8,** 215–219.

Howell, B. F. 1937: Cambrian *Centropleura vermontensis* fauna of northwestern Vermont. *Bull. geol. Soc. Am.* **48,** 1147–1210.

Howell, B. F. 1943: Faunas of the Cambrian Cloud Rapids and Traytown Pond formations of northern Newfoundland. *J. Paleont.* **17,** 236–247.

Hupé, P. 1953: Classe des trilobites. *In* Piveteau, J. (ed.) *Traité de paléontologie* **3,** 44–246. Paris: Masson et Cie.

Hupé, P. 1955: Classification des trilobites. *Annales Paléont.* **41,** 91–325.

Hutchinson, R. D. 1952: Middle Cambrian of the Atlantic realm in eastern Gaspé. *Am. J. Sci.* **250,** 275–280.

Hutchinson, R. D. 1962: Cambrian stratigraphy and trilobite faunas of southeastern Newfoundland. *Bull. geol. Surv. Canada* **88,** 156 pp.

Illing, V. C. 1916 [dated 1915]: Paradoxidian fauna of the Stockingford Shales. *Q. Jl geol. Soc. London* **71,** 386–415.

Ineson, J. R. 1980: Carbonate debris flows in the Cambrian of south-west Peary Land, eastern North Greenland. *Rapp. Grønlands geol. Unders.* **99,** 43–49.

Ineson, J. R. 1985: *The stratigraphy and sedimentology of the Brønlund Fjord and Tavsens Iskappe groups (Cambrian) of Peary Land, eastern North Greenland.* Unpublished Ph.D. thesis, Univ. Keele, 310 pp.

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

Ineson, J. R. & Peel, J. S. 1980: Cambrian stratigraphy in Peary Land, eastern North Greenland. *Rapp. Grønlands geol. Unders.* **99,** 33–42.

Ineson, J. R. & Peel, J. S. 1987: Cambrian platform – outer shelf relationships in the Nordenskiöld Fjord region, central North Greenland. *Rapp. Grønlands geol. Unders.* **133,** 13–26.

Ineson, J. R. & Peel, J. S. unpublished: Cambrian shelf stratigraphy of the Peary Land region, central North Greenland. Manuscript for Grønlands Geologiske Undersøgelse.

Ineson, J. R., Surlyk, F., Higgins, A. K. & Peel, J. S. 1994: Slope apron and deep shelf sediments of the Brønlund Fjord and Tavsens Iskappe Groups (Lower Cambrian – Lower Ordovician) in North Greenland: stratigraphy, facies and depositional setting. *Bull. Grønlands geol. Unders.* **169** (this volume).

International Commission on Zoological Nomenclature. 1985: *International code of zoological nomenclature.* Third edition, 338 pp. London: Internatl Trust Zool. Nomen.

Ivshin, N. K. 1953: [Middle Cambrian trilobites of Kazakhstan, part 1]. Akad. Nauk Kazakh. SSR, Alma-Ata, 226 pp. [In Russian.]

Jago, J. B. 1972a: Biostratigraphic and taxonomic studies of some Tasmanian Cambrian trilobites. Unpublished Ph.D. dissertation, Univ. Adelaide, 448 pp.

Jago, J. B. 1972b: Two new Cambrian trilobites from Tasmania. *Palaeontology* **15,** 226–237.

Jago, J. B. 1990: Cambrian faunas in the terranes of the south-western Pacific part of Gondwana. *Geol. Soc. Austral. Abstr.* **25,** 42–43.

Jell, P. A. 1970: *Pagetia ocellata*, a new Cambrian trilobite from northwestern Queensland. *Mem. Queensland Mus.* **15,** 303–313.

Jell, P. A. 1975: Australian Middle Cambrian eodiscoids with a review of the superfamily. *Palaeontographica* **A 150,** 1–97.

Jell, P. A. 1978: Trilobite respiration and genal caeca. *Alcheringa* **2,** 251–260.

Jell, P. A. 1990: Trilobita. *In* Bengtson, S., Conway Morris, S., Cooper, B. J., Jell, P. A., & Runnegar, B. N. (ed.) Early Cambrian fossils from South Australia. *Mem. Assoc. Australas. Palaeontol.* **9,** 257–322.

Keppie, J. D. 1989: Northern Appalachian terranes and their accretionary history. *In* Dallmeyer, R. D. (ed.) Terranes in the circum-Atlantic orogens. *Spec. Pap. geol. Soc. Am.* **230,** 159–192.

Kobayashi, T. 1935: The Cambro-Ordovician formations and faunas of South Chosen. Palaeontology. Part III. Cambrian faunas of South Chosen with a special study on the Cambrian trilobite genera and families. *J. Fac. Sci., Tokyo Univ.* **4**(2), 49–344.

Kobayashi, T. 1942a: On the Dolichometopinae. *J. Fac. Sci., Tokyo Univ.* **6**(10), 141–206.

Kobayashi, T. 1942b: Miscellaneous notes on the Cambro-Ordovician Geology and Palaeontology VII: An occurrence of dolichometopids in South Chôsen with a summary note on the classification of the Dolichometopinae. *J. geol. Soc. Japan* **49,** 211–218 (*Trans. palaeont. Soc. Japan* **161,** 468–475).

Kobayashi, T. 1943a: Brief notes on the eodiscids I, their classification with a description of a new species and a new variety. *Proc. Imp. Acad. Tokyo* **19,** 37–42.

Kobayashi, T. 1943b: Brief notes on the eodiscids II, phylogeny of the Dawsonidea. *Proc. Imp. Acad. Tokyo* **19,** 43–47.

Kobayashi, T. 1944: On the eodiscids. *Tokyo Imp. Univ., Fac. Sci.*, sec. 2(1), **7,** 1–74.

Kobayashi, T. 1962: The Cambro-Ordovician formations and faunas of South Korea Part IX: Palaeontology VIII: The Machari fauna. *J. Fac. Sci., Tokyo Univ.* **14**(1), 152 pp.

Korobov, M. N. 1973: [Trilobites of the family Conocoryphidae and their importance for the stratigraphy of Cambrian deposits]. *Trudy Akad. Nauk SSSR geol. Inst.* **211,** 176 pp. [In Russian.]

Krashopeeva, P. S. 1958: [Archaeocyathan and archaeocyathan-trilobite horizons of the Altai-Sayan region Cambrian]. *Mater. Geol. zapad.-sib. Kraya* **61,** 105–111. [In Russian.]

Lake, P. 1907: A monograph of the British Cambrian trilobites, part 2. *Monogr. Palaeontogr. Soc., London*, 29–48.

Lake, P. 1931: A monograph of the British Cambrian trilobites, part 6. *Monogr. Palaeontogr. Soc., London*, 121–148.

Lake, P. 1934: A monograph of the British Cambrian trilobites, part 8. *Monogr. Palaeontogr. Soc., London*, 173–196.

Lake, P. 1938: A monograph of the British Cambrian trilobites, part 11. *Monogr. Palaeontogr. Soc., London*, 249–272.

Lake, P. 1940: A monograph of the British Cambrian trilobites, part 12. *Monogr. Palaeontogr. Soc., London*, 273–306.

Lazarenko, N. P. 1962: [New Lower Cambrian trilobites from the Soviet arctic]. *Sb. statei po paleont. biostrat.* **29,** 29–78. [In Russian.]

Lazarenko, N. P. 1965: [Some new Middle Cambrian trilobites from the north of central Siberia]. *Uch. Zap., Paleont. bistrait.* **7,** 14–36. [In Russian.]

Lermontova, E. V. 1940: [Arthropoda]. *In* Vologdin, A. (ed.) [Atlas of the leading forms of the fossil faunas of the USSR.] Vol. 1, 112–157. Moscow, Leningrad: Gos. Izd. Geol. Lit. [In Russian.]

Lermontova, E. V. 1951: [Middle Cambrian trilobites and gastropods from Shody-Mir]. *Trudy Vses. Nauchno-Issled. Geol. Inst.* (VSEGEI). 37 pp. [In Russian.]

Lesley, J. P. 1889: A dictionary of the fossils of Pennsylvania and neighboring states named in the reports and catalogues of the Survey. *Geol. Surv. Pennsylv. Rept* P4, 1283 pp.

Lindström, G. 1901: Researches on the visual organs of the trilobites. *K. Svenska Vetensk.-Akad. Handl.* **34,** 87 pp.

Linnarsson, J. G. O. 1879: Om faunen i kalken med *Conocoryphe exsulans* ('Coronatuskalken'). *Sveriges geol. Unders.* ser. C **35,** 1–35.

Linnarsson, J. G. O. 1883: De undre paradoxideslagren vid Andrarum. *Sver. geol. Unders.* ser. C **54** (1882), 1–40.

Lochman, C. 1947: Analysis and revision of eleven Lower Cambrian trilobite genera. *J. Paleont.* **21,** 59–71.

Lochman, C. 1956: The evolution of some Upper Cambrian and Lower Ordovician trilobite families. *J. Paleont.* **30,** 445–462.

Matthew, G. F. 1886: Illustrations of the fauna of the St. John's Group. *Trans. R. Soc. Canada* **4**(3), 29 pp.

Matthew, G. F. 1887: Illustrations of the fauna of the St. John's Group no. IV – part I. Description of a new species of *Paradoxides* (*Paradoxides regina*). Part II. The smaller trilobites with eyes (Ptychoparidae and Ellipsocephalidae). *Trans. R. Soc. Canada* **5,** 115–166.

Matthew, G. F. 1896: Faunas of the *Paradoxides* beds in eastern North America, no. 1. *Trans. N. Y. Acad. Sci.* **15,** 192–247.

Matthew, G. F. 1897: Studies on Cambrian faunas. *Trans. R. Soc. Canada,* ser. 2, **3**(4), 165–211.

Matthew, G. F. 1899: Studies on Cambrian faunas, no. 3; Upper Cambrian fauna of Mount Stephen, British Columbia. The trilobites and worms. *Trans. R. Soc. Can.* ser. 2, **5**(4), 39–121.

McLaughlin, K. P. & Enbysk, B. B. 1950: Middle Cambrian trilobites from Pend Oreille County, Washington. *J. Paleont.* **24,** 466–471.

McNamara, K. J. 1986a: A guide to the nomenclature of heterochrony. *J. Paleont.* **60,** 4–13.

McNamara, K. J. 1986b: The role of heterochrony in the evolution of Cambrian trilobites. *Biol. Rev.* **61,** 121–156.

McNamara, K. J. & Rudkin, D. M. 1984: Techniques of trilobite exuviation. *Lethaia* **17,** 152–173.

Meek, F. B. 1870: Descriptions of fossils collected by the U.S. Geological Survey under the charge of Clarence King, esq. *Proc. Acad. Sci. Philadelphia* (2nd ser.) **14,** 56–64.

Meek, F. B. 1873: Preliminary paleontological report, consisting of lists and descriptions of fossils, with remarks on the rocks in which they were found. *U.S. geol. Surv. Terr. (Hayden), 6th Ann. Rept.*, 431–518.

Meek, F. B. 1877: Paleontology. *U.S. geol. Expl. 40th Parallel (King)* **4**(2), 197 pp.

Miller, S. A. 1889: *North American geology and paleontology for the use of amateurs, students, and scientists*, 664 pp. Cincinnati: publ. by the author.

Miller, S. A. 1892: *First appendix, 1892*, 665–718. Cincinnati: publ. by the author.

Morris, S. F. 1988: A review of British trilobites, including a synoptic revision of Salter's monograph. *Monogr. Palaeontogr. Soc. London*, 316 pp.

Müller, K. J. & Walossek, D. 1987: Morphology, ontogeny, and life habit of *Agnostus pisiformis* from the Upper Cambrian of Sweden. *Fossils & Strata* **19,** 124 pp.

Nelson, C. A. 1963: Stratigraphic range of *Ogygopsis*. *J. Paleont.* **37,** 244–248.

Nicholas, T. C. 1916 [dated 1915]: On the trilobite fauna of the Middle Cambrian of St. Tudwal's Peninsula. *Q. Jl geol. Soc. London* **71,** 451–472.

Öpik, A. A. 1949: A Middle Cambrian trilobite from Victoria – *Centropleura neglecta* n. sp. *Mining Geol. Jour.* **3,** 55–58.

Öpik, A. A. 1961: The geology and palaeontology of the headwaters of the Burke River, Queensland. *Bull. Bur. Miner. Resour. Australia* **53,** 249 pp.

Öpik, A. A. 1967: The Mindyallan fauna of north-western Queensland. *Bull. Bur. Miner. Resour. Australia* **74**(1), 404 pp.; **74**(2), 167 pp., 67 pls.

Öpik, A. A. 1970: Nepeid trilobites of the Middle Cambrian of northern Australia. *Bull. Bur. Miner. Resour. Australia* **113,** 48 pp.

Öpik, A. A. 1975: Templetonian and Ordian xystridurid trilobites of Australia. *Bull. Bur. Miner. Resour. Australia* **121,** 84 pp.

Öpik, A. A. 1979: Middle Cambrian agnostids: systematics and biostratigraphy. *Bull. Bur. Miner. Resour. Australia* **172**(1), 188 pp.; **172**(2), 67 pls.

Palmer, A. R. 1954: An appraisal of the Great Basin Middle Cambrian trilobite described before 1900. *Prof. Pap. U.S. geol. Surv.* **264D,** 55–86.

Palmer, A. R. 1964: An unusual Lower Cambrian trilobite fauna from Nevada. *Prof. Pap. U.S. geol. Surv.* **483F,** 1–13.

Palmer, A. R. 1966: New Cambrian fossils from Antarctica. *Prof. Pap. U.S. geol. Surv.* **550A,** A95.

Palmer, A. R. 1968: Cambrian trilobites of east-central Alaska. *Prof. Pap. U.S. geol. Surv.* **559B,** 1–115.

Palmer, A. R. 1974: Search for the Cambrian world. *Am. Scient.* **62,** 216–224.

Palmer, A. R. & Gatehouse, C. G. 1972: Early and Middle Cambrian trilobites from Antarctica. *Prof. Pap. U.S. geol. Surv.* **456D,** 1–37.

Palmer, A. R. & Halley, R. B. 1979: Physical stratigraphy and trilobite biostratigraphy of the Carrara Formation (Lower and Middle Cambrian) in the southern Great Basin. *Prof. Pap. U.S. geol. Surv.* **1047,** 1–131.

Palmer, A. R. & Peel, J. S. 1981: Dresbachian trilobites and stratigraphy of the Cass Fjord Formation, western North Greenland. *Bull. Grønlands geol. Unders.* **141,** 46 pp.

Palmer, A: R. & Stewart, J. S. 1968: A paradoxidid trilobite from Nevada. *J. Paleont.* **42,** 177–179.

Peel, J. S. 1982: The Lower Paleozoic of Greenland. *In* Embry, A. F. & Balkwill, H. R. (ed.) Arctic geology and geophysics. *Mem. Can. Soc. petrol. Geol.* **8,** 309–330.

Peel, J. S. & Christie, R. L. 1982: Cambrian–Ordovician platform stratigraphy: correlations around Kane basin. *Meddr Grønland, Geosci.* **8,** 117–135.

Pokrovskaya, N. V. 1959: Trilobitovaya faunai stratigrafiya Kembriyiskikh otlozheniy Tuvy. *Trudy geol. Inst. Leningr.* **27,** 1–198.

Poletaeva, O. K. & Romanenko, E. V. 1970: Nekotorye trilobity srednego i pozdnego Kembriya Altaya. *Paleont. Zhur.* **1970** (2), 72–83. [English translation: Middle and late Cambrian trilobites of the Altay. *Paleont. J.* **4**(2), 216–228.]

Pompeckj, J. F. 1896: Die fauna des Cambrium von Tejrovic und Skrej in Böhmen. *Jahr. d. K. k. geol. Reichsanstalt* **45,** 495–614.

Poulsen, C. 1927: The Cambrian, Ozarkian and Canadian faunas of northwest Greenland. *Meddr Grønland* **71**(2), 233–343.

Poulsen, C. 1946: Notes on the Cambro-Ordovician fossils collected by the Oxford University Ellesmere Land expedition; 1934–35. *Q. Jl geol. Soc. London* **102,** 299–337.

Poulsen, V. 1964: Contribution to the Lower and Middle Cambrian paleontology and stratigraphy of northwest Greenland. *Meddr Grønland* **164**(6), 105 pp.

Poulsen, V. 1969: An Atlantic Middle Cambrian fauna from North Greenland. *Lethaia* **2,** 1–14.

Rasetti, F. 1948a: Lower Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea). *J. Paleont.* **22,** 1–24.

Rasetti, F. 1948b: Middle Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea). *J. Paleont.* **22,** 315–339.

Rasetti, F. 1951: Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains. *Smithson. misc. Collns* **116** (5), 277 pp.

Rasetti, F. 1952: Revision of the North American trilobites of the family Eodiscidae. *J. Paleont.* **26,** 434–451.

Rasetti, F. 1955: Lower Cambrian ptychopariid trilobites from the conglomerates of Quebec. *Smithson. misc. Collns* **128**(7), 35 pp.

Rasetti, F. 1965: Middle Cambrian trilobites of the Pleasant Hill Formation in central Pennsylvania. *J. Paleont.* **39,** 1007–1014.

Rasetti, F. 1967: Lower and Middle Cambrian trilobite faunas from the Taconic sequence of New York. *Smithson. misc. Collns* **152**(4), 111 pp.

Raymond, P. E. 1913: On the genera of the Eodiscidae. *Ottawa Naturalist* **27,** 101–106.

Raymond, P. E. 1937: Upper Cambrian and Lower Ordovician Trilobita and Ostracoda from Vermont. *Bull. geol. Soc. Am.* **48,** 1079–1146.

Raymond, P. E. & Walcott, C. E. 1937: Subclass A. Trilobita Walch. Trilobites. *In* Eastman, C. R. (ed.) *Text-book of palaeontology, adapted from the German of Karl A. von Zittel,* Vol. I. 2nd edition, 692–729. London: MacMillan & Co.

Reed, F. R. C. 1898: Blind trilobites. *Geol. Mag.* (4), **5,** 439–447, 493–506, 552–560.

Resser, C. E. 1935: Nomenclature of some Cambrian trilobites. *Smithson. misc. Collns* **93**(5), 46 pp.

Resser, C. E. 1936: Second contribution to nomenclature of Cambrian trilobites. *Smithson. misc. Collns* **95**(4), 29 pp.

Resser, C. E. 1937a: New species of Cambrian trilobites of the family Conocoryphidae. *J. Paleont.* **11,** 39–42.

Resser, C. E. 1937b: Third contribution to nomenclature of Cambrian trilobites. *Smithson. misc. Collns* **95**(22), 29 pp.

Resser, C. E. 1938: Cambrian System (restricted) of the southern Appalachians. *Spec. Pap. geol. Soc. Am.* **15,** 140 pp.

Resser, C. E. 1939a: The Spence Shale and its fauna. *Smithson. misc. Collns* **97**(12), 29 pp.

Resser, C. E. 1939b: The *Ptarmigania* strata of the northern Wasatch Mountains. *Smithson. misc. Collns* **98**(24), 72 pp.

Resser, C. E. 1942: New Upper Cambrian trilobites. *Smithson. misc. Collns* **103**(5), 136 pp.

Resser. C. E. 1945: Cambrian fossils of the Grand Canyon *In* McKee, E. D. & Resser, C. E. (ed.) *Cambrian history of the Grand Canyon region,* 169–220. Washington: Carnegie Inst.

Reyment, R. A. 1980: Material in the Uppsala collections described by N. P. Angelin (1854) in his 'Palaeontologia Scandinavica', P. I. 'Crustacea formationis transitionis', Lipsiae. Lund. *De rebus in Palaeontologico Museo Upsaliensi collectis. Illustrated catalogue of the type collections of the Palaeontological Museum of the University of Uppsala* **4,** 5–8.

Richter, R. & Richter, E. 1948: Studien im Paläozoikum der Mittelmeer-Länder, 8, Zur Frage des Unter-Kambriums in Nordost-Spanien. *Senckenbergiana* **29,** 23–39.

Robison, R. A. 1964: Late Middle Cambrian faunas from western Utah. *J. Paleont.* **38,** 510–566.

Robison, R. A. 1971: Additional Middle Cambrian trilobites from the Wheeler Shale of Utah. *J. Paleont.* **45,** 796–804.

Robison, R. A. 1972: Mode of life of agnostid trilobites. *Proc. 24 Int. geol. Congr., Montreal* **7,** 33–40.

Robison, R. A. 1976: Middle Cambrian trilobite biostratigraphy of the Great Basin. *Brigham Young Univ. geol. Stud.* **23**(2), 93–109.

Robison, R. A. 1984: Cambrian Agnostida of North America and Greenland; part I, Ptychagnostidae. *Paleontol. Contr. Univ. Kansas Pap.* **109,** 59 pp.

Robison, R. A. 1987: Class Trilobita. *In* Boardman, R. S., Cheetham, A. H. & Rowell, A. J. (ed.) *Fossil invertebrates,* 221–241. Palo Alto, California: Blackwell.

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

Robison, R. A. 1994: Agnostoid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Bull. Grønlands geol. Unders.* **169** (this volume).

Robison, R. A. & Babcock, L. E. 1990: Biogeography of Middle Cambrian trilobites from North Greenland: implications for terrane analysis. *3 Int. Symp. Cambrian System, Novosibirsk, USSR, Abstracts,* 151.

Robison, R. A. & Campbell, D. P. 1974: A Cambrian corynexochid trilobite with only two thoracic segments. *Lethaia* **7,** 273–282.

Romanenko, Y. V. 1985: [Trilobites from the Middle–Upper Cambrian boundary beds of Altai]. *Paleont. Zhur.* **19**(4), 54–63. [In Russian.] [English translation: *Paleont. J.* **19**(4), 64–74.]

Rominger, C. L. 1887: Description of primordial fossils from Mt. Stephens, NW Territory of Canada. *Acad. Nat. Sci. Philadelphia,* Proc. for 1887, 12–19.

Rosova, A. V. 1964: [Biostratigraphy and description of trilobites of the Middle and Upper Cambrian of the northwestern Siberian platform]. Inst. Geol. Geofiz., Akad. Nauk SSSR, Sibir. Otdel., 148 pp. [In Russian.]

Rudkin, D. M. 1979: Healed injuries in *Ogygopsis klotzi* (Trilobita) from the Middle Cambrian of British Columbia. *Occ. Pap. Royal Ontario Mus. Life Sci.* **32,** 8 pp.

Rusconi, C. 1954: Trilobitas Cámbricos de la Quebradita Oblicua, sud del Cerro Aspero. *Revta Mus. Hist. nat, Mendoza* **7,** 3–59.

Rushton, A. W. A. 1966: The Cambrian trilobites from the

Purley shales of Warwickshire. *Monogr. Palaeontogr. Soc. London* **120,** 55 pp.

Rushton, A. W. A. 1974: The Cambrian of England and Wales. *In* Holland, C. H. (ed.) *Lower Paleozoic rocks of the world* **2,** *Cambrian of the British Isles, Norden and Spitsbergen,* 43–121. London: John Wiley & Sons.

Salter, J. W. 1864: On some new fossils from the *Lingula*-flags of Wales. *Q. Jl Geol. soc. London* **20,** 233–241.

Salter, J. W. 1866: A monograph of British trilobites. *Monogr. Palaeontogr. Soc., London,* 129–176.

Scotese, C. R. 1987: Phanerozoic plate tectonic reconstructions. *Paleoceanogr. map. Proj., Univ. Texas, Inst. Geophys., Tech. Rept* **40,** 54 pp.

Scotese, C. R., Bambach, R. K., Barton, C., Van der Voo, R. & Ziegler, A. M. 1979: Paleozoic base maps. *J. Geol.* **87,** 217–277.

Scotese, C. R. & McKerrow, W. S. 1990: Revised world maps and introduction. *In* McKerrow, W. S. & Scotese, C. R. (ed.) Palaeozoic palaeogeography and biogeography. *Mem. geol. Soc. London* **12,** 1–21.

Shah, S. K. & Sudan, C. S. 1982: *Bolaspidella* from the Cambrian of Kashmir and its stratigraphic significance. *J. geol. Soc. India* **23,** 236–245.

Shaw, A. B. 1962: Paleontology of northwestern Vermont. IX. Fauna of the Monkton Quartzite. *J. Paleont.* **36,** 322–345.

Shaw, A. B. 1966: Paleontology of northwestern Vermont. XI. Fossils from the Middle Cambrian St. Albans Shale. *J. Paleont.* **40,** 843–858.

Shimer, H. W. & Shrock, R. R. 1944: *Index fossils of North America,* 837 pp. New York: John Wiley & Sons.

Šnajdr, M. 1957: O novych trilobitech z ceskeho Kambria. *Vestník Ustred. ustav geolog.* **32,** 235–244.

Šnajdr, M. 1958: Trilobiti ceskeho stredního Kambria. *Rozpravy Ustred. ustav geolog.* **24,** 280 pp.

Soper, N. J. & Higgins, A. K. 1985: Thin-skinned structures at the basin-shelf transition in North Greenland. *Rapp. Grønlands geol. Unders.* **126,** 87–94.

Stewart, J. H. & Palmer, A. R. 1967: Callaghan window – a newly discovered part of the Roberts thrust, Toiyabe Range, Lander County, Nevada. *Prof. Pap. U.S. geol. Surv.* **575D,** D56–D63.

Stoyanow, A. 1958: *Sonoraspis* and *Albertella* in the Inyo Mountains, California. *Bull. geol. Soc. Am.* **69,** 347–352.

Strand, T. 1929: The Cambrian beds of the Mjøsen district in Norway. *Norsk geol. Tidsskr.* **10,** 308–365.

Surlyk, F. 1991: Tectonostratigraphy of North Greenland. *Bull. Grønlands geol. Unders.* **160,** 25–47.

Surlyk, F. & Ineson J. R. 1987: Aspects of Franklinian shelf, slope and trough evolution and stratigraphy in North Greenland. *Rapp. Grønlands geol. Unders.* **133,** 41–58.

Suvorova, N. P. 1960: [Cambrian trilobites of eastern Siberian Platform; Olenellidae – Granulariidae]. *Trudy Paleont. Cheskogo Inst.* **84**(2), 1–230. [In Russian.]

Suvorova, N. P. 1964: [Trilobites Corynexochidae and their historical development]. *Trudy Paleont. Inst.* **103,** 319 pp. [In Russian.]

Swofford, D. L. 1989: *PAUP: phylogenetic analysis using parsimony, version 3.0.* 35 pp. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.

Talent, J. A. 1990: The peripatetic fossils: part 5. *Nature* **343,** 405–406.

Termier, G. & Termier, H. 1950: Paléontologie Marocaine II: Invertébrés de l'ère primaire. Fascicule IV: Annélides, arthropodes, échinodermes, conularides et graptolithes. *Maroc, Division des Mines et de la Service Géologique, Notes et Mémoires* **79,** 279 pp.

Thorslund, P. 1949: Notes on *Kootenia* n. sp. and associated *Paradoxides* species from the Lower Middle Cambrian of Jemtland, Sweden. *Sver. geol. Unders.* **C 510,** 3–7.

Vodges, A. W. 1925: Paleozoic Crustacea. The publications and notes on genera and species during the past twenty years, 1895–1917. *Trans. San Diego soc. Nat. Hist.* **3**(1), 1–141.

Walcott, C. D. 1884: The paleontology of the Eureka district, Nevada. *Monogr. U.S. geol. Surv.* **8,** 298 pp.

Walcott, C. D. 1886: Second contribution to the studies on the Cambrian faunas of North America. *Bull. U.S. geol. Surv.* **30,** 369 pp.

Walcott, C. D. 1888: Cambrian fossils from Mount Stephen, northwest territory of Canada. *Am. J. Sci.* 3 ser., **36,** 163–166.

Walcott, C. D. 1889: Description of new genera and species of fossils from the Middle Cambrian. *Proc. U.S. Natl Mus.* **11** (1888), 441–446.

Walcott, C. D. 1908: Mount Stephen rocks and fossils. *Canadian Alpine J.* **1,** 232–248.

Walcott, C. D. 1913: New Lower Cambrian subfauna. *Smithson. misc. Collns* **57**(11), 309–326.

Walcott, C. D. 1916: Cambrian geology and paleontology III: No. 5. Cambrian trilobites. *Smithson. misc. Collns* **64**(5), 301–457.

Walcott, C. D. 1917: Fauna of the Mount Whyte Formation. *Smithson. misc. Collns* **67**(3), 61–114.

Walcott, C. D. 1918: Cambrian geology and paleontology IV, No. 4. Appendages of trilobites. *Smithson. misc. Collns* **67**(4), 115–216.

Walcott, C. D. 1924: Cambrian geology and paleontology V: No. 2. Cambrian and lower Ozarkian trilobites. *Smithson. misc. Collns* **75**(2), 53–60.

Walcott, C. D. 1925: Cambrian geology and paleontology V: No. 3. Cambrian and Ozarkian trilobites. *Smithson. misc. Collns* **75**(3), 61–146.

Westergård, A. H. 1946: Agnostida of the Middle Cambrian of Sweden. *Sver. geol. Unders.* **C 477,** 141 pp.

Westergård, A. H. 1949: *Opsidiscus,* new name replacing *Aulacodiscus* Westergård, 1946. *Geol. Fören. Stockh. Förhandl.* **71,** 606.

Westergård, A. H. 1950: Non-agnostidean trilobites of the Middle Cambrian of Sweden II. *Sver. geol. Unders.* **C 511,** 57 pp.

Westergård, A. H. 1953: Non-agnostidean trilobites of the Middle Cambrian of Sweden III. *Sver. geol. Unders.* **C 526,** 59 pp.

Whiteaves, J. F. 1878: On some primordial fossils from south-eastern Newfoundland. *Am. J. Sci.* **16,** 224–226.

Whitehouse, F. W. 1939: The Cambrian faunas of north-eastern Australia, Part 3. *Mem. Queensland Mus.* N.S. **1,** 179–282.

Wiley, E. O. 1979: An annotated Linnaean hierarchy, with comments on natural taxa and competing systems. *Sys. Zool.* **28,** 308–337.

Woodward, H. 1902: The Canadian Rockies. Part I: On a collection of Middle Cambrian fossils obtained by Edward Whymper, from Mt. Stephen, British Columbia. *Geol. Mag.* (4), **9,** 502–505.

Yanishevski, M. E. 1950: Dryevyyeishii trilovit nishnyecambrian Sinyei Gkini. *Vopr. Paleont. Leningrad Univ.* **1,** 32–40. [In Russian.]

Xiang Liwen & Zhang Tairong. 1985: [Systematic descriptions of trilobites. *In* Stratigraphy and trilobite faunas of the Cambrian in the western part of the northern Tian Shan, Xinjiang.] *Peopl. Republ. China, Minist. Geol. Miner. Resour., Geol. Mem.* ser. **2**(4), 64–243. [In Chinese with English summary.]

Young, G. A. & Ludvigsen, R. 1989: Mid-Cambrian trilobites from the lowest part of the Cow Head Group, western Newfoundland. *Bull. geol. Surv. Canada* **392,** 49 pp.

Zhang, Xi-guang. 1989: Ontogeny of an Early Cambrian eodiscoid trilobite from Henan, China. *Lethaia* **22,** 13–29.

Zhuravleva, I. T. *et al.* 1970: [Concerning knowledge of the Early Cambrian of the southern Tien Shan]. *Trest. 'Tashkentgeologiya' Kompl. geol. poiskobaya eksped., Izd. FAN Uzbeskoy SSR.* 53 pp.

Biogeography and biofacies patterns of Middle Cambrian polymeroid trilobites from North Greenland: palaeogeographic and palaeo-oceanographic implications

Loren E. Babcock

Fossils from Middle Cambrian rocks of Peary Land and Nyeboe Land, North Greenland, show that polymeroid trilobite biofacies were strongly segregated near the shelf margin of Laurentia. Some biofacies include trilobites of Laurentian aspect that lived in warm, relatively shallow water, and other biofacies have trilobites of Baltic aspect that lived in cool, deeper water. Polymeroids in the *Glossopleura* and *Ptychagnostus gibbus* zones are from open-shelf lithofacies and are mostly of Laurentian aspect. Polymeroids in the *Lejopyge laevigata* Zone are from deep, outermost shelf to upper slope lithofacies and are entirely of Baltic aspect. Polymeroids in the *Ptychagnostus atavus* Zone are from an intermediate, outer-shelf setting and are of mixed Laurentian and Baltic aspect. Mixing of polymeroids from different biofacies is inferred to have occurred through downslope movement by localised sediment gravity flows. The presence of segregated trilobite biofacies at the shelf margin of Laurentia is the first evidence for a thermocline in marine waters surrounding Laurentia during the Middle Cambrian, although evidence for a thermocline during the Early and Late Cambrian has been reported previously.

The presence of polymeroids of Baltic aspect in Laurentian rocks of North Greenland has important implications for the analysis of tectonostratigraphic terranes. The presence of cool-water trilobites is not sufficient evidence to conclude that the terrane originated in high palaeolatitudes. Identification of an autochthonous terrane of a continental margin is possible, however, on the basis of fossil assemblages containing mixed biofacies representatives. Provenance identification is possible because the assemblages are expected to include taxa characteristic of warm-water cratonic areas along which the terrane originated.

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Historically, Cambrian trilobite faunas from the circum-Atlantic region have been assigned to either an Atlantic or Pacific faunal province. These provinces have also been called Acado-Baltic and North American, respectively. Several biogeographical studies (e.g., Lochman-Balk & Wilson, 1958; Palmer, 1969, 1972, 1979; Cowie, 1971, 1974; Theokritoff, 1979, 1985; Shergold, 1988) have shown that the Pacific province is characterised by polymeroid trilobites that were mostly endemic to the shelf of Laurentia, whereas the Atlantic province is characterised by polymeroids that were first described from localities in Scandinavia, southern Great Britain, Maritime Canada, or New England.

Trilobites of the Atlantic province have been important in studies of early Palaeozoic biostratigraphy and palaeogeography. Zonations developed for Middle Cambrian trilobites worldwide are commonly compared to the zonation of Sweden's trilobites (Westergård, 1946, 1953). Information about trilobite biogeography is also routinely used to supplement palaeomagnetic, stratigraphic, structural, or other geologic evidence about the configuration and history of continents and oceans during the early Palaeozoic.

The biogeography of Cambrian trilobites has been central to some arguments concerning the origin of tectonostratigraphic terranes in the Appalachian Orogen (see Keppie, 1989 and Horton *et al.*, 1989 for definitions of terranes). The presence of polymeroids having Atlantic affinities in rocks of Maritime Canada and New England (e.g., Howell, 1925; Hutchinson, 1952, 1962; Poulsen & Anderson, 1975; Bergström & Levi-Setti, 1978) has been used to infer the exotic origin of these terranes and subsequent accretion to North America during the middle or late Palaeozoic (see Williams & Hatcher, 1982; Secor

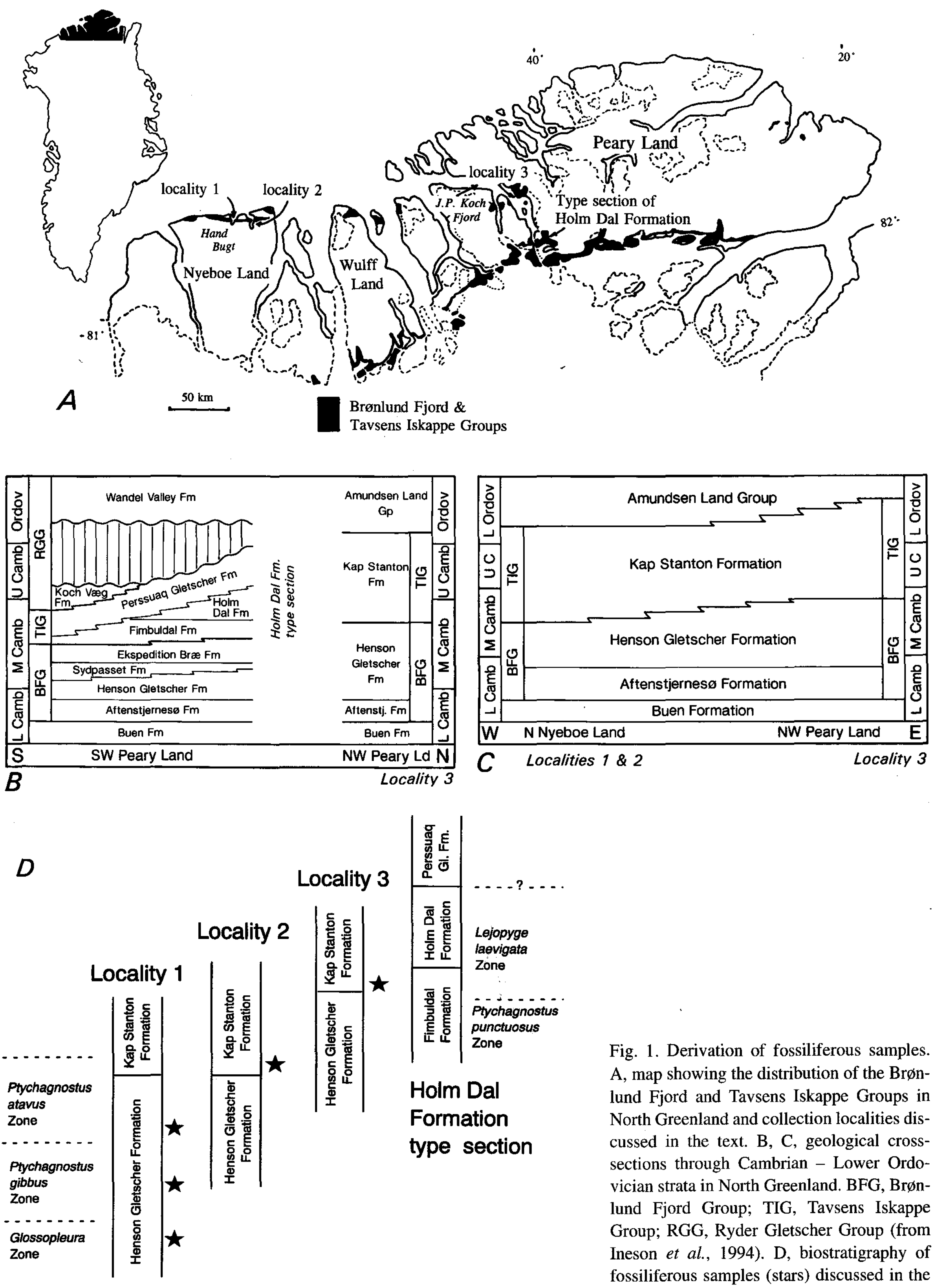


Fig. 1. Derivation of fossiliferous samples. A, map showing the distribution of the Brønlund Fjord and Tavsens Iskappe Groups in North Greenland and collection localities discussed in the text. B, C, geological cross-sections through Cambrian – Lower Ordovician strata in North Greenland. BFG, Brønlund Fjord Group; TIG, Tavsens Iskappe Group; RGG, Ryder Gletscher Group (from Ineson *et al.*, 1994). D, biostratigraphy of fossiliferous samples (stars) discussed in the text.

et al., 1983; Gromet, 1989; Keppie, 1989). Although not all examples of Atlantic trilobites in North America have been associated with accreted terranes, common practice has been to suspect an exotic origin for a terrane that contains such a fauna (see Secor *et al.*, 1983; Gromet, 1989; Horton *et al.*, 1989; Samson *et al.*, 1990), particularly if structural and stratigraphic evidence suggests that it was previously decoupled from North American shelf rocks.

This paper documents the biogeographic and biofacies distributions of polymeroid trilobites from Middle Cambrian rocks of the Henson Gletscher and Kap Stanton formations of Nyeboe Land and Peary Land, North Greenland (Fig. 1). Systematic descriptions are given in an accompanying paper (Babcock, 1994). An additional accompanying paper by Robison (1994) describes agnostoid trilobites from the same formations. The newly described faunas are preserved in open-shelf to deep outermost shelf or upper slope? lithofacies; the palaeogeographic setting is described in a third accompanying paper by Ineson *et al.* (1994). The Henson Gletscher and Kap Stanton formations are coeval in part with the Holm Dal Formation (Peel, 1988), and were in close palaeogeographic proximity (Fig. 1). The Holm Dal Formation contains polymeroid genera that are characteristic of open-shelf environments of Laurentia (Robison, 1988). Middle Cambrian strata in relevant parts of Nyeboe Land and Peary Land are relatively undisturbed structurally, and lithostratigraphic correlations in the region have been made with a high degree of confidence over scores of kilometres (J. S. Peel, personal communication, 1988; cf. Higgins *et al.*, 1991). Fossiliferous localities (Fig. 1) are in native terranes, as defined by Keppie (1989), of the Laurentian palaeocontinent.

The faunas from the Henson Gletscher, Kap Stanton, and Holm Dal formations provide an opportunity to compare open-shelf faunas with those of nearby, deeper marine environments along the Innuitian margin of Laurentia. Sharp biofacies differences between open-shelf lithofacies and deep outermost shelf lithofacies are interpreted to result from differences in either water temperature or environments that covary with temperature. Polymeroids of Laurentian aspect were present in warm shelf waters, whereas polymeroids of Baltic aspect were present in deeper, cool waters.

Biogeographic terminology

The terms Atlantic (or Acado-Baltic) and Pacific (or North American) previously have been used both for the geographic origins of Cambrian trilobite faunas and for faunal provinces. Boundaries of the faunal provinces do not always agree with the boundaries of tectonic plates as presently understood. The terms Pacific and North American, for example, have been used for trilobites or faunas typical of shelf lithofacies of North America as well as Greenland and other regions. The terms Atlantic and Acado-Baltic have been used for trilobites or faunas first described from Scandinavia, Britain, or parts of eastern North America. Similar trilobites, however, also have been found in such other regions as Siberia, Australia, and Antarctica. Poulsen (1969) even applied the term 'Atlantic' to sparse agnostoid assemblages from North Greenland.

To reduce ambiguity, I use separate terms for the geographic origin of a fauna and its aspect. The geographic origin of a fauna is simply the geographic or palaeogeographic locality from which the fauna was collected. The aspect of a fauna refers to a recognised geographic or palaeogeographic region with which an assemblage of taxa is most characteristically associated. It is not necessarily equivalent to a faunal province as previously interpreted. Both types of terms are derived from recognised geographic or palaeogeographic names. The aspect of a fauna, although it bears the name of a geographic region, is recognised as an entity separate from any geographic region. As an example, a fauna collected from Laurentia is a Laurentian fauna, but it may contain taxa of Laurentian, Baltic, Gondwanan, or other aspect.

Palaeogeography and biogeography

Current palaeogeographic reconstructions (e.g., Scotese, 1987; Scotese & McKerrow, 1990) show the Cambrian world as comprising four principal cratonic areas, Laurentia, Baltica, Gondwana, and Siberia, as well as other smaller tectonic plates (Fig. 2). Terminology and definitions of tectonic plates used in this paper generally follow those of Scotese *et al.* (1979). Exceptions are England, Acadia, and Armorica, which are defined according to Young (1986).

Laurentia included cratonic North America, Greenland, western Newfoundland, northern Ireland and Scotland, Spitsbergen, western Norway, and the Chukotsk Peninsula of eastern Siberia. During the Cambrian, Laurentia was in tropical latitudes. At times, extensive carbonate platforms developed in surrounding warm, shallow seas. Development of the platforms led to marked differentiation of trilobite faunas in restricted-shelf and open-shelf habitats (e.g., Palmer, 1972, 1973; Robison, 1976).

Siberia, which consisted of the present-day Siberian platform, Mongolia, Manchuria, and Taymyr, was also in low latitudes during the Cambrian. It too was the site of carbonate-platform development during parts of the Cambrian.

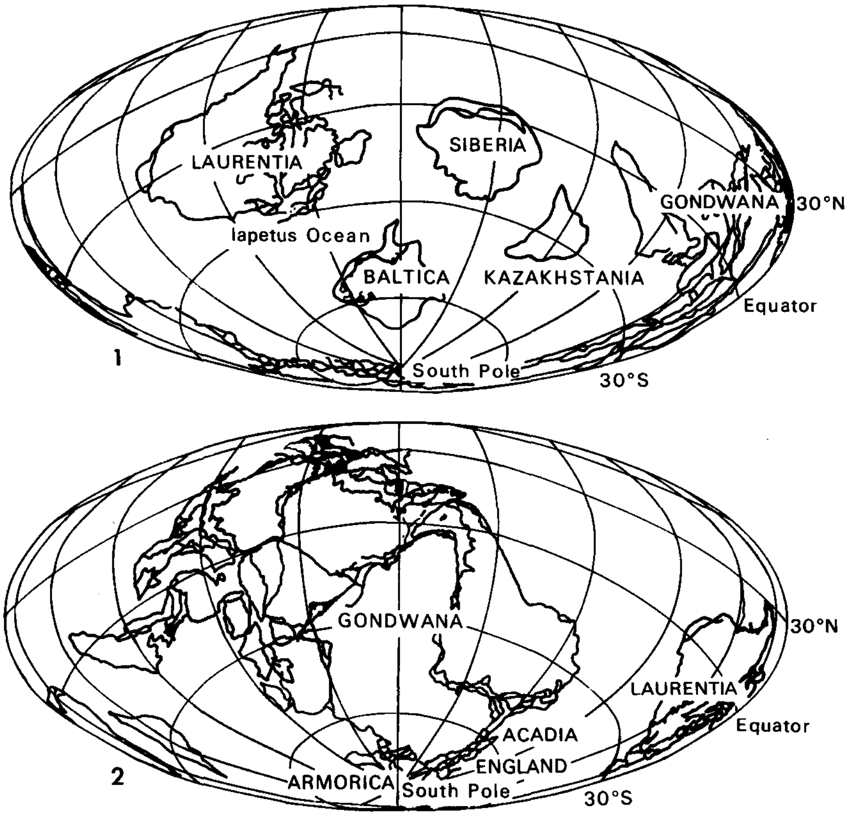


Fig. 2. Maps of reconstructed Middle Cambrian paleogeography (after Scotese & Denham, 1988). Outlines of present-day geographic areas are included for reference. The view is from 30 degrees south latitude. 1, View emphasising the relationships of Laurentia, Baltica, and Siberia. 2, View emphasising Gondwana and the peri-Gondwanan terranes.

Baltica, which consisted of north-western Europe exclusive of the British Isles and western Norway, was probably in moderately high to high southern latitudes during most of the Cambrian (Scotese *et al.*, 1979; Scotese, 1987; Scotese & McKerrow, 1990; Torsvik *et al.*, 1991; but see Smith *et al.*, 1981). Shelf sedimentation was dominated by fine-grained siliciclastics, including alum shales. Carbonate units comprise a minor part of the Cambrian section.

Major components of Gondwana were South America, Africa, Florida, Arabia, Turkey, Iran, Afghanistan, India, Madagascar, Australia, and parts of Antarctica. Gondwana extended from tropical to polar latitudes. England (Wales, southern Ireland, and southern England), Acadia (eastern New England and Maritime Canada except for eastern Nova Scotia and western Newfoundland), and Armorica (Bohemia, southern Germany, France, Iberian Peninsula, northern Morocco, and eastern Nova Scotia) were three important peri-Gondwanan terranes. All were located in polar or subpolar latitudes of the North African sector of Gondwana.

Other important terranes include those of Kazakhstania (including present-day Kazakhstan, Tien Shan, and the Aral Sea area) and present-day China. Recent evidence suggests that Kazakhstania is composed of several fused microcontinental blocks, and includes an archipelago located in low palaeolatitudes (Cook & Taylor, 1989; Cook *et al.*, 1991). Considerable uncertainty remains concerning the palaeogeographic positions of tectonostratigraphic terranes of China.

A variety of geophysical, stratigraphic, structural, petrologic, and palaeontologic evidence has been used to assess plate-tectonic history. Faunal evidence is of particular importance in the lower Palaeozoic because other reliable geologic and geophysical evidence can be more difficult to obtain than for other intervals of the Phanerozoic. Distributions of fossils played a major role in Wilson's (1966) hypothesis of a proto-Atlantic Ocean, as well as in many subsequent studies of the history of the Iapetus Ocean. Distributional data continue to be important in current arguments about the definition and history of terranes in the circum-Atlantic region (e.g., Williams & Hatcher, 1982; Secor *et al.*, 1983; Samson *et al.*, 1990) and elsewhere.

Studies of the distribution of Cambrian trilobites worldwide (e.g., Palmer, 1969, 1972, 1979; Jell, 1974; Burrett & Richardson, 1980; Shergold, 1988; Robison, 1991) have demonstrated that shelf seas of the major cratonic areas of Laurentia, Baltica, Siberia, and Gondwana tended to have relatively large numbers of endemic trilobite genera and species. Endemism is strongest among polymeroids, most of which were probably benthic. Most genera and many species of the largely pelagic agnostoids had cosmopolitan distributions in world oceans (e.g., Robison, 1972, 1984, 1988; Öpik, 1979).

Patterns of distribution of early Palaeozoic trilobites in the circum-Atlantic region have traditionally been used to define Atlantic (or Acado-Baltic) and Pacific (or North American) faunal provinces (e.g., Palmer, 1969, 1972; Poulsen, 1969; Cowie, 1971, 1974). Biotic exchange between these regions has been generally thought to have been limited by several factors, including the time available for larval migration across geographic distances (McKerrow & Cocks, 1976; Burrett & Richardson, 1980; Fortey & Cocks, 1986). In this interpretation, Iapetus may have been wide during the Cambrian (Conway Morris & Rushton, 1988). A trend of increasing similarity between North American and western European faunas during the Ordovician and Silurian has been inferred to result from the progressive closure of Iapetus and the elimination of faunal barriers (McKerrow & Cocks, 1976).

Studies of distributional patterns in the circum-Atlantic region, like most that have used biogeographic data to help determine the configuration of plates during the early Palaeozoic, have incorporated three major assumptions (Taylor & Forester, 1979). First, faunal elements were assumed to have been largely restricted to shallow-shelf seas of single continental blocks. Second, the shallow-shelf seas were surrounded by deeper oceans, which inhibited dispersal. Third, the degree of faunal dissimilarity between areas is assumed to have been a function of their past geographic separation (also see Sneath & McKenzie, 1973). Mounting evidence from the distributions of trilobites (Palmer, 1973; Fortey, 1975; Taylor, 1976, 1977; Cook & Taylor, 1975; Taylor & Cook, 1976; Ludvigsen, 1978; Taylor & Forester, 1979; Babcock & Robison, 1989; Robison & Babcock, 1990) and other organisms (Skevington, 1974; Sweet and Bergström, 1974; Barnes & Fåhraeus, 1975; Bergström & Carnes, 1976; Bergström, 1977; Fortey & Cocks, 1986) indicates that these assumptions are not always valid. Factors of the marine environment other than distance have probably had an important influence on the degree of faunal resemblance between geographic regions. Such factors may include latitudinal climatic gradients (e.g., Ekman, 1953; Valentine, 1973) and differences between shelf seas and the deep sea (e.g., Hedgpeth, 1957; Bruun, 1957; Menzies *et al.*, 1973; Benson, 1975, 1988; Taylor, 1977). The effects of both of these factors on faunal distributions have been disregarded or accorded minor importance in many studies of early Palaeozoic faunas. Also, they have often been disregarded when synthesising geological and geophysical data for palaeogeographic reconstructions.

Biogeographic affinities of North Greenland polymeroid trilobites

Middle Cambrian rocks of North Greenland contain polymeroid trilobite assemblages of both Laurentian and Baltic aspect. Most polymeroids described by Poulsen (1927), Poulsen (1964), Palmer & Peel (1981), and Robison (1988) have closest affinities with trilobites that are characteristic of open-shelf areas of Laurentia. Polymeroids identified by Poulsen (1969) from Nyeboe Land, including *Eodiscus punctatus* and a paradoxidid (possibly *Centropleura*) have closest affinities with taxa characteristic of cratonic areas of Baltica. The observed geographic distributions of polymeroid taxa identified from the Henson Gletscher and Kap Stanton formations are summarised in Tables 1 to 4.

All genera in new Geological Survey of Greenland (GGU) collections (Babcock, 1994, but see also a preliminary notice by Fletcher *et al.*, 1988) from the *Glossopleura* Zone (Table 1) are widely distributed in open-shelf lithofacies of Laurentia. One genus, *Kootenia*, is also known from shelf lithofacies of present-day Asia and Australia. Two species, *Ogygopsis klotzi* and *Glossopleura walcotti*, have been recognised elsewhere in Laurentia.

In addition to its occurrence in North Greenland, *O. klotzi* is known from the Stephen Formation of British Columbia (Rasetti, 1951), the Metalline Formation of Washington (McLaughlin & Enbysk, 1950), the Miller Mountain Formation of Nevada (Nelson, 1963), the Cow Head boulders of western Newfoundland (Young & Lud-

Table 1. Distributions of polymeroid genera in the Glossopleura *Zone of the Henson Gletscher Formation*

TAXA	AN	AM	GB	AL	CR	OL
Glossopleura walcotti	–	–	s	–	G	–
Kootenia nodosa	G	G	G	G	G	G
Ogygopsis klotzi	s	s	s	G	s	–
Syspacephalus sp. 3	G	G	G	–	G	–

Observed geographic distributions of polymeroid genera (G) or genera and species (s) identified in the *Glossopleura* Zone of the Henson Gletscher Formation (hyphen indicates absence of a genus). Abbreviations of geographic regions are AN, northern Appalachia (western Newfoundland and Quebec); AM, middle Appalachia (New York and Pennsylvania); GB, Great Basin (Utah, Nevada, and California); AL, east-central Alaska; CR, Canadian Rocky Mountains; and OL, tectonic blocks other than Laurentia.

Table 2. Distributions of polymeroid genera in the Ptychagnostus gibbus *Zone of the Henson Gletscher Formation*

TAXA	AN	AM	GB	AL	CR	OL
Bathyuriscus sp.	G	G	G	G	G	–
Bolaspidella sp.	–	G	G	G	–	G
Olenoides sp.	G	G	G	–	G	G
Syspacephalus sp. 2	G	G	G	–	G	–
Zacanthoides sp.	G	G	G	G	G	–

Observed geographic distributions of polymeroid genera (G) identified in the *Ptychagnostus gibbus* Zone of the Henson Gletscher Formation (hyphen indicates absence of a genus). Abbreviations of geographic regions are AN, northern Appalachia (western Newfoundland and Quebec); AM, middle Appalachia (New York and Vermont); GB, Great Basin (Utah, Nevada, and California); AL, east-central Alaska; CR, Canadian Rocky Mountains; and OL, tectonic blocks other than Laurentia.

vigsen, 1989), and the Kinzers Formation of Pennsylvania (Campbell, 1971). Each occurrence represents an open-shelf setting near the ocean-facing side of a carbonate platform. Other occurrences of *Ogygopsis* (Nelson, 1963; Palmer & Halley, 1979) indicate that the genus is most commonly associated with platform-edge environments (Palmer & Halley, 1979).

G. walcotti was first described from the Cape Wood Formation of Inglefield Land, North-West Greenland. Later, abundant material was reported from the Carrara Formation of Nevada and California (Palmer & Halley, 1979). *Glossopleura* was previously identified primarily from restricted-shelf lithofacies (e.g., Robison, 1976; Palmer & Halley, 1979), but examination of collections at the University of Kansas and the U.S. National Museum of Natural History indicates that some species were more eurytopic than previously thought. In the Henson Gletscher Formation, *G. walcotti* is associated with such characteristic open-shelf taxa as *Ogygopsis* and *Syspacephalus*. *Kootenia*, with which it is also associated, is eurytopic (Robison, 1976).

Genera of polymeroids in GGU collection 298970 from the *Ptychagnostus gibbus* Zone have strongest affinities with genera from open-shelf environments of Laurentia (Table 2). *Syspacephalus* and *Zacanthoides* are known only from Laurentia. *Bolaspidella* is known with certainty from Laurentia (Robison, 1988) and the Precordillera terrane of Mendoza, Argentina (Poulsen, 1960). The Precordillera terrane may have been derived from Laurentia (Ramos *et al.*, 1986; Robison, 1991). The reported occurrence of *Bolaspidella* from Kashmir (Shah & Sudan, 1982) is probably in error (Robison, 1988). Except for *Zacanthoides*, which is eurytopic, all the genera are most commonly associated with open-shelf lithofacies. *Olenoides* inhabited open-shelf sites in Laurentia but was also present in Siberia, Kazakhstania, and Gondwana. *Kootenia* is a eurytopic genus that is common in Laurentia, but like some other dorypygids, it was rather widely distributed in low palaeolatitudes. Finally, *Eodiscus* was widespread in open-shelf settings around much of the world. Functional analyses of morphology and wide geographic distributions indicate that most eodiscids were pelagic or perhaps planktonic (Jell, 1975).

Table 3. Distributions of polymeroid genera in the Ptychagnostus atavus *Zone of the Henson Gletscher and Kap Stanton formations*

TAXA	AN	AM	GB	CR	AL	CM	SW	EN	SP	AU
Bathyuriscus concavus	G	G	G	G	G	–	–	–	–	–
Corynexochus? sp.	–	–	–	–	G	–	G	G	–	–
Costadiscus minutus	–	–	–	–	–	–	–	–	–	–
Dasometopus groenlandicus	–	–	–	–	–	–	G	–	G	–
Eodiscus scanicus	–	–	–	–	–	s	s	s	–	–
Hartshillia inflata	–	–	–	–	–	G	–	s	G	–
Olenoides cf. *O. convexus*	s	G	G	G	–	–	–	–	G	–
Opsidiscus longispinus	–	–	–	–	–	–	G	–	–	G
Parasolenopleura aculeata	–	–	–	–	–	–	s	G	–	–
Solenopleurella transversa?	–	s	–	–	–	G?	G	G?	–	–
Syspacephalus sp. 1	G	G	G	G	–	–	–	–	–	–

Observed geographic distributions of polymeroid genera (G) or genera and species (s) identified in the *Ptychagnostus atavus* Zone of the Henson Gletscher and Kap Stanton formations (hyphen indicates absence of a genus). Abbreviations of geographic regions are AN, northern Appalachia (western Newfoundland and Quebec); AM, middle Appalachia (New York and Pennsylvania); GB, Great Basin (Utah and Nevada); AL, east-central Alaska; CR, southern Canadian Rocky Mountains; CM, maritime Canada except for western Newfoundland; SW, Sweden; EN, England south of the Caledonian suture; SP, Siberian platform; and AU, Australia.

Table 4. Distributions of polymeroid genera in the Lejopyge laevigata *Zone of the Kap Stanton Formation*

TAXA	AM	GB	SW	NO	EN	CM	BO	BI	SP	AU
Anomocarina excavata	–	–	s	s	–	–	–	s	s	–
Centropleura angelini	G	G	s	–	G	G	G	G	G	G
Centropleura loveni	G	G	s	–	G	G	G	G	s	G
Elyx trapezoidalis	G	–	G	G	–	G	–	–	G	–
Solenopleura bucculenta	G?	–	s	G	G	–	–	–	G	–

Observed geographic distributions of polymeroid genera (G) or genera and species (s) identified in the *Lejopyge laevigata* Zone of the Kap Stanton Formation (hyphen indicates absence of a genus). Abbreviations of geographic regions are AM, middle Appalachia (New York and Vermont); GB, Great Basin (Nevada); SW, Sweden; NO, Norway; EN, England south of the Caledonian suture; CM, maritime Canada except for western Newfoundland; BO, Bohemia; BI, Bennett Island; SP, Siberian platform; and AU, Australia.

This, together with the numerous pelagic agnostoids in GGU 298970 (Robison, 1994), suggests that trilobites in this collection had unrestricted access to the open ocean.

Polymeroids in new collections (Babcock, 1994) representing the *Ptychagnostus atavus* Zone are of mixed Laurentian and Baltic aspect (Table 3), and those in the *Lejopyge laevigata* Zone are entirely of Baltic aspect (Table 4). Patterns in the palaeogeographic distributions of polymeroids occurring in these two zones in North Greenland were explored using multivariate methods. Results, summarised in the following section, reveal a strong distinction between major faunal associations (biofacies) and some subtle but important associations.

Multivariate analyses of trilobite collections

Multivariate methods were used to explore patterns of faunal association among polymeroid trilobites from selected localities in North Greenland, North America, Scandinavia, and Great Britain. Faunas analysed are from the *Ptychagnostus atavus* and *Lejopyge laevigata* zones.

Binary (presence–absence) data were analysed using cluster analysis (CA) and multidimensional scaling (MDS). Analyses were performed using version 3 of the SYSTAT statistical package (SYSTAT, Inc.) on an Apple Macintosh II computer. Cluster analysis was used to separate data sets into discrete groups (see Hazel, 1970, 1977). In Q-mode analyses, objects (collections) were related to each other on the basis of their attributes (genera). In R-mode analyses, attributes (genera) were related to each other on the basis of the objects (collections) in which they occur. Clustering was performed on Euclidean distance coefficients using average linkage and unweighted pair group arithmetic means. Euclidean distance has the advantage of producing a distribution that closely approximates to the binomial probability distribution with data that are not sparse (C. G. Maples, personal communication, 1990). Therefore, values of Euclidean coefficients can be tested for statistical significance by using binomial probabilities (see Archer & Maples, 1987; Maples & Archer, 1988). Confidence intervals established for clusters on data from the *L. laevigata* and *P. atavus* zones are listed in Table 5.

To test further the reliability of clusters, MDS was used in a manner analogous to R mode. The rationale for using it is that CA can distort between-group relationships, although relationships within compact groups are likely to be accurate (Kruskal, 1964a, 1964b; Hazel, 1977). MDS distributes distortion evenly between large and small distances (Hazel, 1977). Lastly, fidelity and constancy indices (Hazel, 1970, 1977; Hood & Robison, 1988) were calculated for all genera in principal clusters as measures of how well they characterise a particular cluster. A fidelity index measures the extent to which a taxon is confined to samples of a cluster. Fidelity (F) is defined by

$$F_{ji} = N_i / \Sigma N_i \star 10$$

where N_i is the number of collections in each cluster in

Table 5. Confidence intervals for clusters of trilobite presence-absence data

ZONE	N	*P*<0.10	*P*<0.05	*P*<0.01
Lejopyge laevigata	27	0.75	0.81	0.89
Ptychagnostus atavus	21	0.77	0.83	0.90

Confidence intervals for clusters of trilobite presence-absence data produced in Q-mode and R-mode, derived from a comparison of Euclidean distance coefficients to a binomial distribution (data provided by C. G. Maples). Samples on which cluster analysis was performed are from the *Lejopyge laevigata* and *Ptychagnostus atavus* zones. Coefficients greater than the listed values are considered to be statistically dissimilar. N indicates the number of columns in the data matrices.

which the species is present, and ΣN_i is the total number of collections in which the species is present. A constancy index measures the extent to which a taxon is present in samples of a cluster compared to all possible occurrences. Constancy (C) is defined by

$$C_{ji} = N_i / T_i \star 10$$

where T_i is the total number of samples in a cluster. Both indices are rounded to the nearest whole number. Genera having both high fidelity and high constancy indices best define a cluster (Hazel, 1970).

Data on genera from 9 localities in the *L. laevigata* Zone and 10 localities in the *P. atavus* Zone were analysed. Collections chosen for analysis are either new (GGU 298969, 301313, and 319790) or from the published literature. Data compiled from published sources are mostly based on well-described collections but some identifications by Kindle (1982) are considered to be preliminary. For some taxa, nomenclatural revisions have been made to bring names into conformity with current taxonomic concepts. Except for GGU collections, collections were agglomerative and commonly included taxa pooled from two or more geographically close localities. Binary data, rather than frequency data, were chosen because taphonomic factors, including effects of preservation, diagenesis, and collecting, can render comparisons between frequency data suspect (Archer & Maples, 1987). Samples used are not of uniform size, and are not necessarily from the same ecological context (see Kaesler, 1966). Furthermore, the numerical abundance of preserved and identified taxa probably does not faithfully represent the original faunal composition (see Staff *et al.*, 1986). Trilobite data from other parts of the world were not included in the analysis partly because of differences in some generic concepts as applied outside of North America and western Europe. Also, the tendency of many shelf-dwelling Cambrian polymeroid genera to be endemic to a region or continent would produce data sets containing few presences and a large number of absences. Such sparse data will tend to skew calculations to emphasise differences between localities. Furthermore, they will tend to truncate zones of statistical significance (Maples & Archer, 1988).

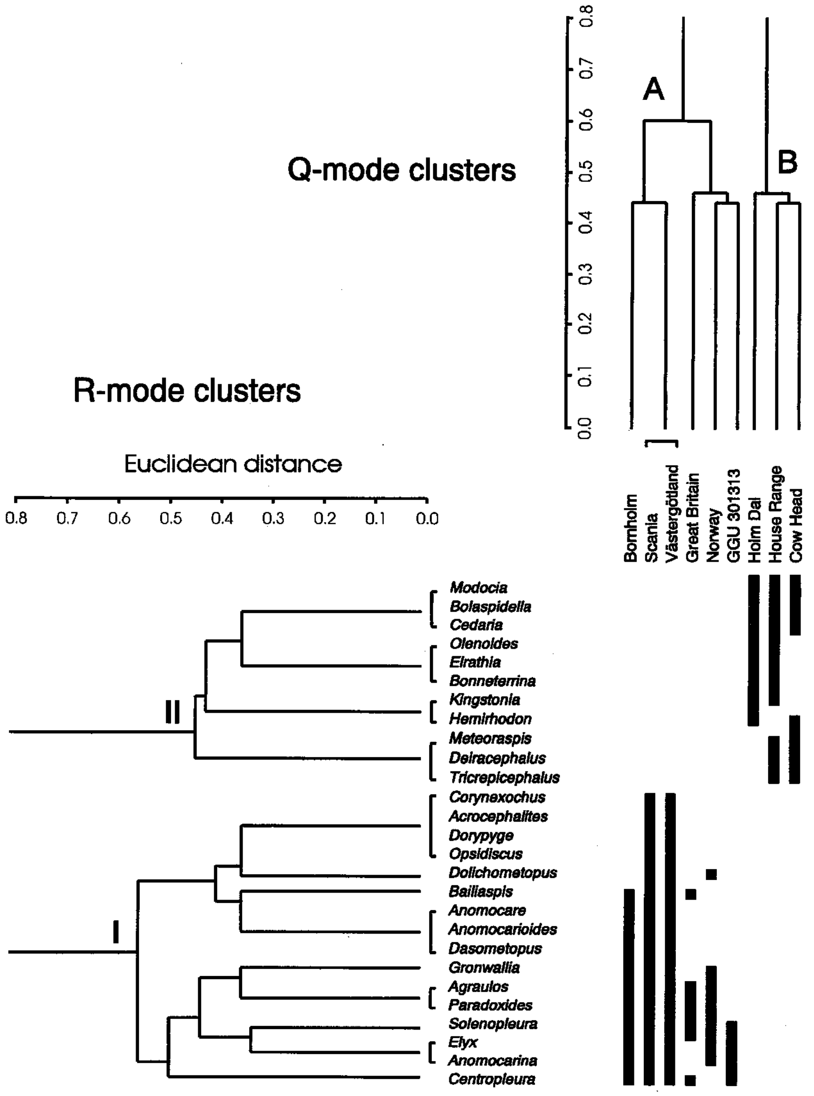
Complete and reduced data matrices were analysed. The complete data matrix for samples from the *L. laevigata* Zone consisted of 75 genera from nine localities (collections). For the *P. atavus* Zone it consisted of 37 genera from 10 localities. In the reduced data matrices, genera present in only one collection were eliminated from analyses. Such taxa may be important constituents of individual collections, but they yielded little comparative information and tended to increase distance coefficients between collections. The smaller matrices contained 27 genera from the *L. laevigata* Zone and 21 genera from the *P. atavus* Zone. Both the complete and reduced matrices produced similar patterns of clusters. Different values of coefficients evidently resulted from collections that contained large numbers of genera not present in other collections. To illustrate better the similarities among collections, only results based on the smaller data matrices are discussed.

Analysed collections from the *L. laevigata* Zone include two from North Greenland (GGU 301313, herein; and Holm Dal Formation, Robison, 1988), four from Scandinavia (Scania and Västergötland in Sweden, Bornholm in Denmark, and Norway; Westergård, 1946, 1953), one from southern Great Britain (Thomas *et al.*, 1984), one from eastern Canada (Cow Head Group of Quebec, Kindle, 1982), and one from western North America (House Range, Utah; Robison, 1964, personal communication, 1989; Beebe, 1989).

Q-mode CA produced two principal clusters containing similar genera (Fig. 3, A, B). The average distance coefficient between clusters A and B is 0.82. The null hypothesis that there is no difference between these clusters is rejected at the 0.05 level (see Table 5). Cluster A includes GGU 301313 and collections from localities in Scandinavia and Great Britain south of the Caledonian suture. Cluster B includes collections from the Holm Dal Formation of North Greenland, the House Range of Utah, and the Cow Head boulders of western Newfoundland. The principal clusters correspond to localities that have polymeroid genera entirely of Baltic and Laurentian aspect, respectively. The lack of taxonomic overlap between collections may be partially a function of the collections chosen for study, but in large measure it seems to be indicative of a fundamental difference between trilobite biofacies. Examination of available literature shows that less than five percent of all polymeroids recorded from shelf lithofacies in the *L. laevigata* Zone of Laurentia are also present in coeval rocks of Baltica and the peri-Gondwanan terranes.

R-mode cluster analysis produced two primary clusters (Fig. 3, I, II) that show which groups of genera are responsible for the Q-mode clusters. The average distance coefficient between clusters I and II is 0.82. The null hypothesis that there is no difference between clusters is rejected at the 0.05 level (see Table 5). Cluster I contains 16 genera that are either geographically widespread or restricted to sites in North Greenland, Scandinavia, or Great Britain. Genera that previously have been observed only in Baltica include *Acrocephalites*, *Dolichometopus*, and *Gronwallia*. *Agraulos*, *Bailiaspis*, and *Paradoxides* have wider distributions but are best known from regions that were in high palaeolatitudes, including

Fig. 3. Cluster analysis of data on polymeroid collections from the *Lejopyge laevigata* Zone of North Greenland and selected localities in North America, Scandinavia, and Great Britain. Data are plotted in order formed by Q-mode clustering of collections and R-mode clustering of genera. Primary clusters are labelled with Roman numerals and uppercase letters. Cluster A contains genera of Baltic aspect, and cluster B contains genera of Laurentian aspect.



Baltica, Gondwana, and peri-Gondwanan terranes. *Anomocarina*, *Anomocarioides*, and *Dasometopus* are known from sites in Baltica and Siberia. *Dasometopus* and *Anomocarina* are reported by Babcock (1994) from North Greenland. *Elyx* has now been observed in Baltica, Siberia, Acadia, and North Greenland. From published records, *Centropleura*, *Corynexochus*, *Opsidiscus*, and *Solenopleura* all have relatively wide distributions, although not necessarily during the *L. laevigata* Biochron.

Cluster II contains eleven genera which are restricted to Laurentia except *Olenoides* and *Modocia*. *Olenoides* is diverse in Laurentia but was also present in shelf seas of Siberia, Kazakhstania, China, and the Precordillera terrane of Argentina. It, like some other genera assigned to the Dorypygidae (Poulsen *in* Harrington *et al.*, 1959: O217–O219), seems to have been widely distributed in low palaeolatitudes. *Modocia* is a common and diverse genus in Laurentia, and the only verified occurrence other than Laurentia is a single specimen from England (Rushton, 1978).

Results using MDS (Fig. 4) are in close agreement with results of the CA. Genera that formed clusters in R-mode analysis form discrete, rather compact groups in two-dimensional MDS. The first dimension represents a contrast between the 16 genera of Baltic aspect and the 11 genera of Laurentian aspect. The second dimension primarily represents a contrast between more widespread genera and less widespread ones.

Fidelity and constancy indices for clusters (Fig. 3) are listed in Table 6. Cluster I contains 16 genera that define cluster A and have been collected from localities in Scandinavia, Great Britain, or Peary Land, North Greenland

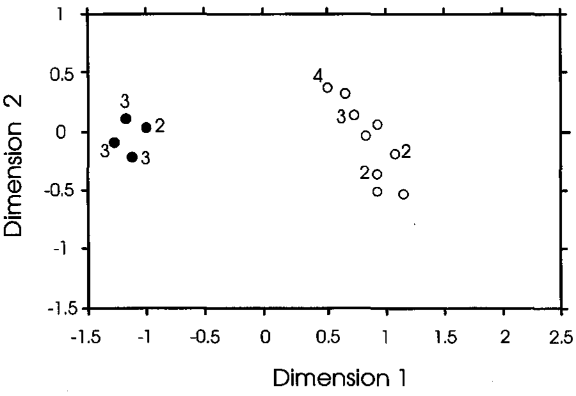


Fig. 4. Scattergram of coordinates of genera analysed by multidimensional scaling. Taxa analysed are from the *Lejopyge laevigata* Zone. Open circles correspond to polymeroid genera of Baltic aspect as defined in Q-mode cluster analysis, and closed circles correspond to genera of Laurentian aspect. A numeral next to a circle indicates the number of genera that are stacked vertically at that point.

(GGU 301313). All have high fidelity indices. Genera that also have high constancy indices are *Agraulos*, *Anomocarina*, *Bailiaspis*, *Centropleura*, *Elyx*, *Gronwallia*, *Paradoxides*, and *Solenopleura*. Some genera appear to have been largely restricted to Baltica and England but, as indicated above, this is an artifact of the localities that were chosen for analysis. Cluster II includes genera that define cluster B and that are most common in open-shelf lithofacies of North America. All have high fidelity and constancy indices. Except for *Olenoides* and *Modocia*, all are restricted to Laurentia. Extra-Laurentian samples containing these genera, however, were not included in the analysis.

Trilobite samples from the *L. laevigata* Zone of the Kap Stanton Formation are interpreted to represent autochthonous associations of trilobites in deep, outermost shelf or possibly upper slope lithofacies. Specimens are commonly articulated and fragile fossils preserved parallel to bedding in dark, organic-rich lime mudstone. Disarticulated sclerites are also common, but are generally unbroken. Some specimens represent undisturbed moulted exoskeletons. Specimens range from small meraspides to large holaspides. Little post-mortem or post-moulting transportation of sclerites is indicated. Furthermore, the presence of undisturbed laminae indicates little or no faunal mixing by bioturbation. All four genera and four of five species present in these collections (Table 4) are also present in coeval rocks of Scandinavia. Some genera or species are found in open-shelf lithofacies of southern Great Britain, Siberia, Kazakhstan, Australia, or China. None of the genera is present in coeval rocks of the Holm Dal Formation (see Robison, 1988). This is remarkable in view of the fact that section 3, where trilobites of Baltic aspect were found, is only about 40 km from the type section of the Holm Dal Formation in Peary Land (Fig. 1). The Holm Dal Formation contains trilobites primarily of Laurentian aspect (see Robison, 1988). Major tectonic dislocation has not been observed in this region (Fletcher *et al.*, 1988; Higgins *et al.*, 1991). Rocks of the Holm Dal Formation represent an inferred low energy, open-shelf environment (Ineson, 1988); water depths were probably significantly less than those in which the sediments of the lower Kap Stanton Formation, as seen along J. P. Koch Fjord, were deposited.

Collections analysed from the *P. atavus* Zone include two from North Greenland (GGU 298969 and 319790; Babcock, 1994), one from western North America (House Range, Utah; Robison, 1964 and unpublished data), two from eastern Canada (Cow Head Group, Quebec, Kindle, 1982; and south-eastern Newfoundland,

Table 6. Fidelity and constancy indices for polymeroids from the Lejopyge laevigata *Zone*

	CLUSTER A			CLUSTER B		
	F	C	N	F	C	N
Modocia	–	–	–	10	10	3
Bolaspidella	–	–	–	10	10	3
Cedaria	–	–	–	10	10	3
Olenoides	–	–	–	10	7	2
Elrathia	–	–	–	10	7	2
Bonneterrina	–	–	–	10	7	2
Kingstonia	–	–	–	10	7	2
Hemirhodon	–	–	–	10	7	2
Meteoraspis	–	–	–	10	7	2
Deiracephalus	–	–	–	10	7	2
Tricrepicephalus	–	–	–	10	7	2
Corynexochus	10	3	2	–	–	–
Acrocephalites	10	3	2	–	–	–
Dorypyge	10	3	2	–	–	–
Opsidiscus	10	3	2	–	–	–
Dolichometopus	10	5	3	–	–	–
Bailiaspis	10	7	4	–	–	–
Anomocare	10	5	3	–	–	–
Anomocarioides	10	5	3	–	–	–
Dasometopus	10	5	3	–	–	–
Gronwallia	10	7	4	–	–	–
Agraulos	10	8	5	–	–	–
Paradoxides	10	8	5	–	–	–
Solenopleura	10	10	6	–	–	–
Elyx	10	8	5	–	–	–
Anomocarina	10	8	5	–	–	–
Centropleura	10	8	5	–	–	–

Fidelity (F) and constancy (C) indices for polymeroids in two Q-mode clusters shown in Fig. 3 from the *Lejopyge laevigata* Zone. The number of collections containing a genus is listed under N. A hyphen indicates the absence of a genus from a cluster.

Hutchinson, 1962), three from Scandinavia (Norway, Västergötland, and Bornholm; Westergård, 1946, 1953), and one from southern Great Britain (Thomas *et al.*, 1984). The GGU collections include specimens in both mudstone and packstone. Genera preserved in both lithologies were grouped together in this analysis because all that are present in mudstone are also present in packstone.

CA in Q mode produced two primary clusters (Fig. 5, A, B) that show major faunal differences between collections containing polymeroids of Laurentian and Baltic aspect. The Euclidean distance coefficient between clusters A and B is 0.76, which is considered to be of borderline statistical significance at the 0.1 level (see Table 5). Cluster A contains collections from Great Britain, south-eastern Newfoundland, Scandinavia (Västergötland, Bornholm, Scania, and Norway), and North Greenland (GGU 298969 and 319790). Cluster B contains collections from the House Range, Utah, and the Cow Head Group, western Newfoundland.

GGU collections 298969 and 319790 from North Greenland and collections from boulders of the Cow Head Group of Newfoundland all consist of mixed assemblages of polymeroids having Laurentian and Baltic aspect. All polymeroids in the GGU collections preserved in mudstone are of Baltic aspect and probably represent trilobites indigenous to the deep, outermost shelf lithofacies. Most polymeroids preserved in packstone are also of Baltic aspect. One of 5 genera (20 percent) in GGU 298969 and 2 of 6 genera (33 percent) in GGU 319790, however, are of Laurentian aspect. Most polymeroids from the Cow Head collections are of Laurentian aspect but 4 of 10 genera (40 percent) are of Baltic aspect. A few trilobites of Laurentian or Baltic aspect may have coexisted in some places, but the differences between taxa preserved in mudstone and packstone in North Greenland

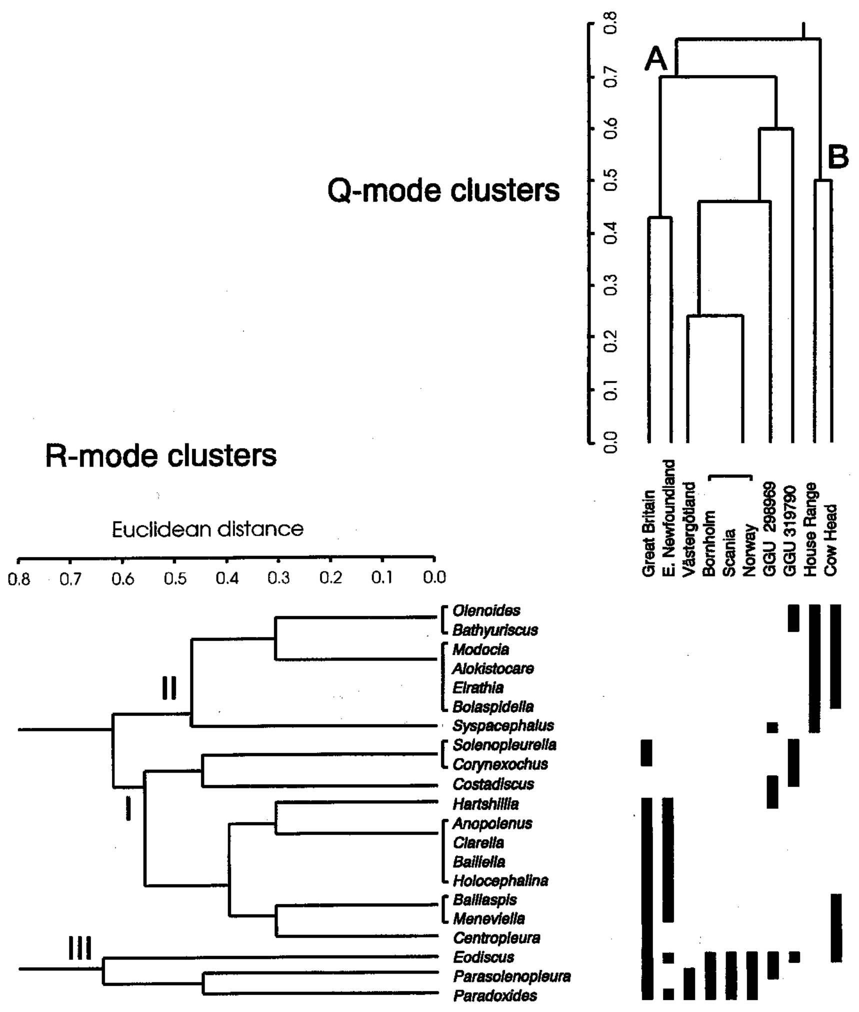


Fig. 5. Cluster analysis of data on polymeroid collections from the *Ptychagnostus atavus* Zone of North Greenland and selected localities in North America, Scandinavia, and Great Britain. Data are plotted in order formed by Q-mode clustering of collections and R-mode clustering of genera. Primary clusters are labelled with Roman numerals and uppercase letters. Cluster A contains genera of Baltic aspect (except *Olenoides*, *Bathyuriscus*, and *Syspacephalus*), and cluster B contains genera of Laurentian aspect.

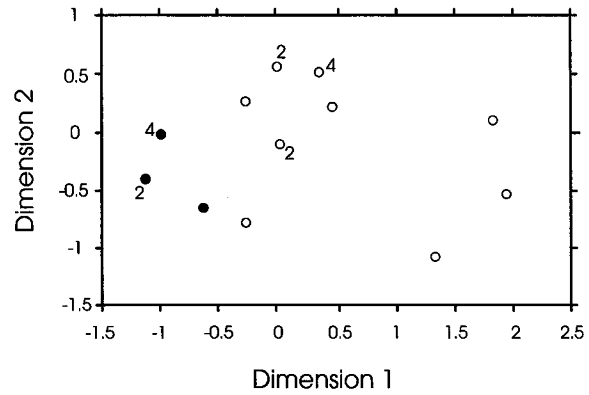


Fig. 6. Scattergram of coordinates of genera analysed by multidimensional scaling. Taxa analysed are from the *Ptychagnostus atavus* Zone. Open circles correspond to polymeroid genera of Baltic aspect as defined in Q-mode cluster analysis, and closed circles correspond to genera of Laurentian aspect. A numeral next to a circle indicates the number of genera that are stacked vertically at that point.

suggest that biofacies of polymeroids were strongly differentiated.

Stratigraphic and sedimentologic evidence suggest that trilobites in GGU collections 298969 and 319790 and collections from the Cow Head Group have been mixed by sedimentary processes. All of these collections contain disarticulated and fragmented trilobite sclerites and occur in deeper-water successions that accumulated basinward of steep-rimmed, shallow-water carbonate platforms. The specimens from North Greenland that are preserved in packstone are crudely size-sorted, and are interpreted to have been redeposited by sediment gravity flows (see Ineson, 1980 and discussion in Ineson *et al.*, 1994). The Cow Head material was collected from limestone breccia that was inferred to have been deposited by gravity flow (Hubert *et al.*, 1977; Hiscott & James, 1985; James & Stevens, 1986). Boulders in the Cow Head Group represent several depositional lithofacies (Kindle, 1982; James & Stevens, 1986).

R-mode CA produced three primary clusters (Fig. 5, I–III). Cluster I contains all of the genera of Baltic aspect except *Eodiscus*, *Parasolenopleura*, and *Paradoxides*, which form cluster III. Genera in clusters I and III are responsible for cluster A produced in Q mode. Cluster II contains seven genera characteristic of open-shelf sites in Laurentia. These taxa are responsible for cluster B produced in Q mode. The average Euclidean distance coefficient between clusters I and II is 0.63. The null hypothesis that there is no difference between clusters I and II cannot be rejected ($P > 0.1$; see Table 5). The rather low distance coefficient is probably due mostly to the presence of three mixed collections (GGU 298969, GGU 319790, and Cow Head Group) in the analysis. The distance coefficient between clusters I + II and III is 0.82, which is considered to be of borderline statistical significance at the 0.1 level (see Table 5). Cluster III contains three genera that were evidently widespread. The cluster has a high level of dissimilarity from the other clusters probably because the contained genera are widely distributed among localities that contain polymeroids of Baltic aspect.

Results of MDS (Fig. 6) illustrate the relatively lower distance coefficients between clusters containing polymeroids of mostly Baltic aspect (Fig. 5, A) and Laurentian aspect (Fig. 5, B), compared to samples analysed from the *L. laevigata* Zone. Genera that comprise clusters A and B form loose clusters. Most of the taxa in cluster B have coordinates near those in cluster A. *Eodiscus*, *Paradoxides*, and *Parasolenopleura* have coordinates that are most distant from taxa in cluster A. The first axis has been fitted primarily to the contrast between polymeroids of Laurentian and Baltic aspect. The second axis is fitted primarily to the contrast between more widespread and less widespread genera.

Fidelity and constancy indices for polymeroids from

Table 7. Fidelity and constancy indices for polymeroids from the Ptychagnostus atavus *Zone*

	CLUSTER A			CLUSTER B		
	F	C	N	F	C	N
Olenoides	–	–	–	7	10	3
Bathyuriscus	–	–	–	7	10	3
Modocia	–	–	–	10	10	2
Alokistocare	–	–	–	10	10	2
Elrathia	–	–	–	10	10	2
Bolaspidella	–	–	–	10	10	2
Syspacephalus	–	–	–	5	5	2
Solenopleurella	10	3	2	–	–	–
Corynexochus	10	3	2	–	–	–
Costadiscus	10	3	2	–	–	–
Hartshillia	10	4	3	–	–	–
Anopolenus	10	3	2	–	–	–
Clarella	10	3	2	–	–	–
Bailiella	10	3	2	–	–	–
Holocephalina	10	3	2	–	–	–
Bailiaspis	7	3	3	–	–	–
Meneviella	7	3	3	–	–	–
Centropleura	5	1	2	–	–	–
Eodiscus	9	9	8	–	–	–
Parasolenopleura	10	8	6	–	–	–
Paradoxides	10	8	6	–	–	–

Fidelity (F) and constancy (C) indices for polymeroids in two Q-mode clusters shown in Fig. 5 from the *Ptychagnostus atavus* Zone. The number of collections containing a genus is listed under N. A hyphen indicates the absence of a genus from a cluster.

the *P. atavus* Zone are listed in Table 7. Except for *Centropleura*, all 14 genera that produced cluster A have high fidelity indices. Those that also have high constancy indices are *Eodiscus*, *Paradoxides*, and *Parasolenopleura*. All genera in cluster B except *Syspacephalus* have high fidelity and constancy values. *Syspacephalus* is restricted to Laurentia, but disarticulated sclerites have been found in one mixed assemblage, GGU 298969, in which most polymeroids are of Baltic aspect.

In summary, collections from packstone beds of the *P. atavus* Zone of North Greenland (e.g., GGU 298969 and 319790) contain polymeroids of both Laurentian and Baltic aspects. Most examined specimens are disarticulated and fragmented. Polymeroids in the intervening mudstones are entirely of Baltic aspect, and tend to be found articulated. Trilobites in mudstone are interpreted to have been indigenous to the deep outermost shelf. Those in packstone, however, have probably been mixed by sediment gravity-flow processes introducing skeletal material typical of outer-shelf environments into the deeper-water setting.

Environmental relationships of trilobites

Middle Cambrian strata of the *L. laevigata* and *P. atavus* zones of North Greenland include biofacies dominated by polymeroids having either Laurentian or Baltic aspect. Trilobites of Baltic aspect were evidently indigenous to the deep outermost shelf or upper basin slope, whereas those of Laurentian aspect inhabited open-shelf lithofacies. Resedimentation of trilobite sclerites has resulted in the mixing of trilobites of different aspects in some beds of the *P. atavus* Zone (Fig. 7).

In recent years, faunal differences in Cambrian rocks have been commonly attributed to environmental gradients in which temperature played a major role (Cook & Taylor, 1975, 1977; Taylor, 1976, 1977; Taylor & Cook 1976; Taylor & Forester, 1979; Theokritoff, 1979; Conway Morris & Rushton, 1988; Shergold, 1988; Babcock & Robison, 1989; Robison & Babcock, 1990). Stratigraphic and biogeographic evidence has been presented to show that some oceans were thermally stratified during the Early Cambrian (Theokritoff, 1979) and the Late Cambrian (e.g., Taylor & Forester, 1979), just as they are during the Holocene (e.g., Benson, 1975, 1988). The results presented in this paper suggest that ocean waters

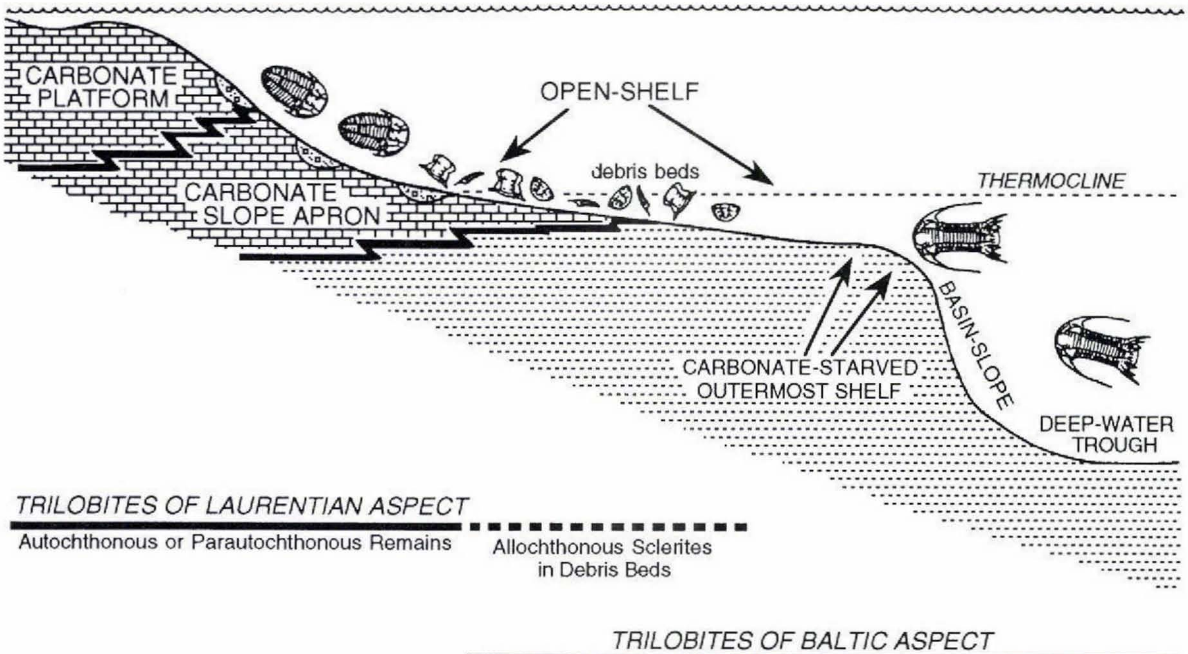


Fig. 7. Model of the Innuitian margin of Laurentia off present-day North Greenland during the Middle Cambrian illustrating the relationships of physiography, sedimentation patterns, and trilobite biofacies. Polymeroid trilobites of Baltic aspect (represented by *Centropleura*, right) are inferred to have lived below the permanent thermocline. Fossils of Baltic trilobites are preserved in lime mudstone and are commonly articulated. Polymeroids of Laurentian aspect (represented by *Bathyuriscus*, left) are inferred to have lived in warm shallower water above the thermocline but their disarticulated remains (represented by isolated sclerites of *Bathyuriscus*) were dispersed basinward by gravity displacement of sediment and redeposited in debris beds.

surrounding Laurentia were also thermally stratified during the Middle Cambrian (Fig. 7). Other postulated explanations for biogeographic barriers, including a deep-water basin (see Wilson, 1966; Cowie, 1971) and a land barrier (Ulrich & Schuchert, 1902), were reviewed by Theokritoff (1979). Theokritoff rejected the idea that a deep-water basin was alone sufficient to act as a biogeographic barrier on both uniformitarian arguments and evidence about the distribution of some Early Cambrian trilobites. The notion of a land barrier was rejected on the basis of biogeographic and stratigraphic evidence.

The terms thermosphere and psychrosphere (Bruun, 1957) describe the divisions of the world oceans that are respectively above and below the permanent thermocline. In low and intermediate latitudes, warmer, less dense waters of the thermosphere, which are characterised by temperatures higher than 10°C, float above cooler, more dense waters of the psychrosphere, which are characterised by temperatures lower than 10°C (Bruun, 1957; Benson, 1975). In present-day, high-latitude shelf areas, the thermosphere is not present.

Based on an analysis of modern isopod biofacies, Taylor & Forester (1979) found that faunas indigenous to warm shelves in low latitudes show strong similarities to other warm-water faunas and strong dissimilarities to faunas in cool marine waters. Those from cool waters show a high degree of similarity whether they are in high latitudes or in low latitudes below the permanent thermocline. It is likely that thermal stratification of water masses during parts of the early Palaeozoic similarly affected the biogeographic distributions of trilobites (see Taylor & Forester, 1979). The mostly endemic shelf faunas of Laurentia are inferred to have been adapted to warm water, whereas faunas described from shelf areas of Baltica and southern Gondwana or from peri-Gondwanan terranes located in south-polar regions are inferred to have been adapted to cool water.

Taylor & Forester (1979) listed three criteria that they considered to be necessary to demonstrate the presence of a two-layered thermally stratified Palaeozoic ocean. They are (1) evidence of deep-water environments, (2) strong biofacies differences between indigenous faunas of deep-water environments and those of adjacent warm shelves, and (3) widely distributed deep-water faunas that show greatest taxonomic resemblance to faunas in other deep-water environments and shallow-water environments of high latitudes.

Rocks and faunas of the *L. laevigata* and *P. atavus* zones of North Greenland meet Taylor & Forester's criteria. First, deep-water shelf environments, basinward of the carbonate platform are represented by the Henson Gletscher and Kap Stanton formations. Rocks from those units are interpreted (Ineson *et al.*, 1994) to represent open-shelf to deep, outermost shelf (or possibly basin-slope) environments along the Innuitian margin of Laurentia.

Second, indigenous deeper-water polymeroid faunas of North Greenland show strong dissimilarities with coeval faunas from the adjacent warm-water Laurentian shelf. Polymeroid faunas of the *L. laevigata* Zone that were indigenous to putative deep, outermost shelf environments do not share any genera or species with a fauna reported from the coeval Holm Dal Formation (Robison, 1988), which was deposited in an inferred low energy, open-shelf setting (Ineson, 1988). Trilobites described from the type section of the Holm Dal Formation were collected approximately 40 km south of locality 3 (Fig. 1), indicating that faunal changes between the shelf and slope were abrupt.

Shallower water faunas from the *P. atavus* Zone of North Greenland were not available for comparison. Nevertheless, comparison of trilobites in mudstone and packstone from GGU collections 298969, 319789, and 319790 indicate a strong faunal dissimilarity between putative open-shelf-dwelling and deep, outermost shelf-dwelling polymeroids. Some polymeroids found as resedimented particles in GGU collections are interpreted to have been derived from open-shelf settings where polymeroids of Laurentian aspect predominated. Two species, *Olenoides* cf. *O. convexus* and *Solenopleurella transversa*, have been previously described from open-shelf sites elsewhere in Laurentia. Except for the eodiscid *Costadiscus*, which is known only from North Greenland, polymeroids in undisturbed mudstone are exclusively of Baltic aspect.

Finally, polymeroids indigenous to putative deep, outermost shelf or upper slope environments of the *L. laevigata* and *P. atavus* zones in North Greenland are taxonomically most similar to faunas from shallow-shelf environments of cool, high-latitude areas of Baltica, Acadia, Armorica, and England. Some taxa, including *Centropleura*, *Eodiscus*, and solenopleurids, are also known from deep-water Laurentian sites in north-western Vermont (Howell, 1937; Shaw, 1966), south-eastern New York (Rasetti, 1967) and central Nevada (Stewart & Palmer, 1967; Palmer & Stewart, 1968; Babcock, 1990). Indigenous deep-water polymeroids of the Henson Gletscher and Kap Stanton formations evidently did not also inhabit shallower water environments of the Laurentian shelf. Where trilobites of mixed Laurentian and Baltic aspect have been found in the same beds, evidence suggests that they were brought together by taphonomic processes.

Polymeroids of the *P. atavus* Zone in Nyeboe Land support stratigraphic and structural evidence (Fletcher *et al.*, 1988; Higgins *et al.*, 1991; Surlyk, 1991) that these rocks are *in situ* and were not accreted by plate collision. Minimal fragmentation and lack of size sorting suggest that specimens preserved in mudstone probably are autochthonous or parautochthonous to environments at continental margins, including deep, outermost shelf and perhaps slope areas. Specimens in packstone, which are more fragmented and size sorted, are interpreted to have been redeposited. Many were probably carried basinward from proximal shelf sites by gravity flows. Analogous deposits containing resedimented trilobites that were near the Laurentian continental margin have been described from the Upper Cambrian of central Nevada (Cook & Taylor, 1975, 1977; Taylor, 1976; Taylor & Cook, 1976). There, redeposited warm-water trilobites of Laurentian aspect are interbedded with indigenous trilobites having an Asian aspect. Other possible continental slope deposits that contain resedimented trilobites of mixed provincial affinities (Taylor & Forester, 1979) include some in the Taconic sequence of New York (Bird & Theokritoff, 1968; Bird & Rasetti, 1968), the Cow Head Group of western Newfoundland (Babcock, 1991; see Kindle, 1982), and the Collier Shale of Arkansas (Hart *et al.*, 1987; Hohensee & Stitt, 1989).

Geological implications

During the Middle Cambrian, separate polymeroid biofacies developed in warm waters of the Laurentian open-shelf and in cool waters of deeper, outermost shelf to uppermost basin or slope? areas. Most genera and almost all species found in open-shelf lithofacies were endemic to Laurentia. Important exceptions are genera of the Dorypygidae (especially *Dorypyge*, *Kootenia* and *Olenoides*) which are widespread in shelf facies of some tectonic plates that were in low palaeolatitudes. Most genera and species of polymeroids from deeper-water habitats of North Greenland seem to be the same as those from cool, shallow-shelf sites of Baltica or peri-Gondwanan terranes.

The presence of polymeroids of Baltic aspect in Laurentian rocks of Nyeboe Land and Peary Land, North Greenland, has important implications for reconstructing the history of tectonic blocks during the early Palaeozoic. It is evident that the presence of trilobites of Baltic aspect in a suspect terrane attached to a tectonic plate that was in low palaeolatitudes is not sufficient evidence in itself to conclude that the terrane is exotic. An exotic terrane is one that has moved from a distant source and subsequently accreted to another tectonic plate. A native terrane, by comparison, can include deep-shelf, slope or basinal areas adjacent to or on the tectonic plate with which it is now associated. The presence of cool-water trilobites of Baltic aspect in a suspect terrane has been commonly used as evidence of an origin in high latitudes. Some cool-water biofacies, however, are similar to each other regardless of latitude or depth and a suspect terrane containing such trilobites could in fact have an origin either in high latitudes or in deep water of low latitudes.

Cool waters evidently were avenues for the dispersal of some organisms (Taylor & Forester, 1979). On this account, the degree of taxonomic dissimilarity among cool-water faunas of different regions is not necessarily a function of the palaeogeographic distance between those areas. Thus, conclusions about the latitudinal separation of tectonic blocks during the geological past that are based on differences between warm-water and cool-water biofacies are suspect. Conclusions about palaeolatitude based on faunas and lithofacies from shelf successions are more reliable, but palaeomagnetic evidence remains the best indicator of the original latitudinal positions of terranes.

The presence of mixed assemblages of warm-water and cool-water biofacies in the *P. atavus* Zone of North Greenland illustrates a method by which autochthonous terranes of the outer continental shelf or slope can be identified (Babcock, 1991). Taphonomic, sedimentologic, and stratigraphic evidence needs to be examined before assemblages of mixed aspect can be determined to represent organisms that either lived together or were redeposited as bioclastic debris from ecologically separate biofacies. In addition to improving interpretations of the tectonic history of suspect terranes, study of mixed assemblages in continental shelf and slope environments may help to improve the resolution of biostratigraphic correlations between separate continents.

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References

Archer, A. W. & C. G. Maples. 1987: Monte Carlo simulation of selected binomial similarity coefficients (I): effect of number of variables. *Palaios* **2**, 609–617.

Babcock, L. E. 1990: Biogeography, phylogenetics, and systematics of some Middle Cambrian trilobites from open-shelf to basinal lithofacies of North Greenland and Nevada. Unpublished Ph.D. dissert., Univ. Kansas, 222 pp.

Babcock, L. E. 1991: Debris beds containing mixed faunal representatives from shelf-margin biofacies: a tool for use in terrane analysis. *Geol. Soc. Am. Abstr. Prog.* **23**(3), 2.

Babcock, L. E. 1994: Polymeroid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Bull. Grønlands geol. Unders.* **169** (this volume).

Babcock, L. E. & Robison, R. A. 1989: Paleobiogeographic significance of Middle Cambrian trilobites from North Greenland. *Geol. Soc. Am. Abstr. Prog.* **21**(6), A340.

Barnes, C. R. & Fåhraeus, L. E. 1975: Provinces, communities, and the proposed nektobenthic habit of Ordovician conodontophorids. *Lethaia* **8**, 133–149.

Beebe, M. A. 1989: Unusual preservation of Cambrian trilobites in the Weeks Formation of Utah. *Geol. Soc. Am. Abstr. Prog.* **21**(6), A71.

Benson, R. H. 1975: The origin of the psychrosphere as recorded in changes of deep-sea ostracode assemblages. *Lethaia* **8**, 69–83.

Benson, R. H. 1988: Ostracods and palaeoceanography. *In* De Decker, P., Colin, J.-P. & Peypouquet, J.-P. (ed.) *Ostracoda in the earth sciences*, 1–26. Amsterdam: Elsevier.

Bergström, J. & Levi-Setti, R. 1978. Phenotypic variation in the Middle Cambrian trilobite *Paradoxides davidis* Salter at Manuels, SE Newfoundland. *Geolog. Palaeont.* **12**, 1–40.

Bergström, S. M. 1977: Early Paleozoic conodont biostratigraphy in the Atlantic borderlands. *In* Swain, F. M. (ed.) *Stratigraphic micropaleontology of Atlantic basin and borderlands*, 85–110. New York: Elsevier.

Bergström, S. M. & Carnes, J. B. 1976: Conodont biostratigraphy and paleoecology of the Holston Formation (Middle Ordovician) and associated strata in eastern Tennessee. *In* Barnes, C. R. (ed.) Conodont paleoecology. *Spec. Pap. geol. Assoc. Canada* **15**, 27–57.

Bird, J. M. & Rasetti, F. 1968: Lower, Middle, and Upper Cambrian faunas in the Taconic sequence of eastern New York: stratigraphic and biogeographic significance. *Spec. Pap. geol. Soc. Am.* **113**, 66 pp.

Bird, J. M. & Theokritoff, G. 1968: Mode of occurrence of fossils in the Taconic allochthon. *Spec. Pap. geol. Soc. Am.* **101**, 248 only.

Bruun, A. F. 1957: Deep sea and abyssal depths. *In* Hedgpeth, J. W. (ed.) Treatise on marine ecology and paleoecology, Vol. 1, Ecology. *Mem. geol. Soc. Am.* **67**, 641–672.

Burrett, C. & Richardson, R. 1980: Trilobite biogeography and Cambrian tectonic models. *Tectonophys.* **63**, 155–192.

Campbell, L. D. 1971: Occurrence of '*Ogygopsis* shale' fauna in southeastern Pennsylvania. *J. Paleont.* **45**, 437–440.

Conway Morris, S. & Rushton, A. W. A. 1988: Precambrian to Tremadoc biotas in the Caledonides. *In* Harris, A. L. & Fettes, D. J. (ed.) The Caledonian–Appalachian Orogen. *Spec. Publ. geol. Soc. Lond.* **38**, 93–109.

Cook, H. E. & Taylor, M. E. 1975: Early Paleozoic continental margin sedimentation, trilobite biofacies, and the thermocline, western United States. *Geology* **3**, 559–562.

Cook, H. E. & Taylor, M. E. 1977: Comparison of continental slope and shelf environments in the Upper Cambrian and lowest Ordovician of Nevada. *In* Cook, H. E. & Enos, P. (ed.) Deep-water carbonate environments. *Spec. Publ. Soc. Econ. Paleont. Mineral.* **25**, 51–81.

Cook, H. E. & Taylor, M. E. 1989: Evolution of early Paleozoic carbonate seamount, Malyi Karatau Range, southern Kazakhstan, USSR: new evidence for early history of Kazakhstania. *Abstr. 28 int. geol. Congr., Washington D.C.* **1**, 322 only.

Cook, H. E. *et al.* 1991: Comparison of two early Paleozoic carbonate submarine fans – western United States and southern Kazakhstan, Soviet Union. *In* Cooper, J. D. & Stevens, C. H. (ed.) Paleozoic paleogeography of the Western United States – II. *Pacific section, Soc. Econ. Paleont. Mineral.*, 847–872.

Cowie, J. W. 1971: Lower Cambrian faunal provinces. *In* Middlemiss, F. A., Rawson, P. F. & Newall, G. (ed.) Faunal provinces in space and time. *Spec. Publ. geol. Soc. Lond.* **4,** 31–46.

Cowie, J. W. 1974: The Cambrian of Spitsbergen and Scotland. *In* Holland, C. H. (ed.) *Lower Palaeozoic rocks of the world, Vol. 2, Cambrian of the British Isles, Norden and Spitsbergen,* 125–155. London: J. Wiley & Sons.

Ekman, S. 1953: *Zoogeography of the sea,* 417 pp. London: Sidgwick and Jackson.

Fletcher, T. P., Higgins, A. K. & Peel, J. S. 1988: A Balto-Scandian Middle Cambrian fauna from Peary Land, North Greenland. *Rapp. Grønlands geol. Unders.* **137**, 118 only.

Fortey, R. A. 1975: Early Ordovician trilobite communities. *Fossils & Strata* **4**, 331–352.

Fortey, R. A. & Cocks, L. R. M. 1986: Marginal faunal belts and their structural implications, with examples from the lower Paleozoic. *Jl geol. Soc. Lond.* **143**, 151–160.

Gromet, L. P. 1989: Avalonian terranes and late Paleozoic tectonism in southeastern New England; constraints and problems. *In* Dallmeyer, R. D. (ed.) Terranes in the circum-Atlantic orogens. *Spec. Pap. geol. Soc. Am.* **230**, 193–211.

Harrington, H. J. *et al.* 1959: Systematic descriptions. *In* Moore, R. C. (ed.) *Treatise on invertebrate paleontology,* part O, *Arthropoda* **1,** O170–O540. Lawrence: Geol. Soc. Am. and Kansas Univ. Press.

Hart, W. D., Stitt, J. H., Hohensee, S. R. & Ethington, R. L. 1987: Geological implications of Late Cambrian trilobites from the Collier Shale, Jessieville area, Arkansas. *Geology* **15**, 447–450.

Hazel, J. E. 1970: Binary coefficients and clustering in biostratigraphy. *Bull. geol. Soc. Am.* **81**, 3237–3252.

Hazel, J. E. 1977: Use of certain multivariate and other techniques in assemblage zonal biostratigraphy: examples using Cambrian, Cretaceous, and Tertiary benthic invertebrates. *In* Kauffman E. G. & Hazel, J. E. (ed.) *Concepts and methods of biostratigraphy*, 187–212. Stroudsburg: Dowden, Hutchinson & Ross.

Hedgpeth, J. W. 1957: Marine biogeography. *In* Hedgpeth, J. W. (ed.) Treatise on marine ecology and paleoecology, Vol. 1, Ecology. *Mem. geol. Soc. Am.* **67**, 359–382.

Higgins, A. K., Ineson, J. R., Peel, J. S., Surlyk, F. & Sønderholm, M. 1991: Lower Palaeozoic Franklinian Basin of North Greenland. *Bull. Grønlands geol. Unders.* **160**, 71–139.

Hiscott, R. N. & James, N. P. 1985: Carbonate debris flows, Cow Head Group, western Newfoundland. *J. sed. Petrol.* **55**, 735–745.

Hohensee, S. R. & Stitt, J. H. 1989: Redeposited *Elvinia* Zone (Upper Cambrian) trilobites from the Collier Shale, Ouachita Mountains, west-central Arkansas. *J. Paleont.* **63**, 857–879.

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.

Horton, J. W., Jr., Drake, A. A., Jr. & Rankin, D. W. 1989: Tectonostratigraphic terranes and their Paleozoic boundaries in the central and southern Appalachians. *In* Dallmeyer, R. D. (ed.) Terranes in the circum-Atlantic orogens. *Spec. Pap. geol. Soc. Am.* **230**, 213–245.

Howell, B. F. 1925: The faunas of the Cambrian *Paradoxides* beds at Manuels, Newfoundland. *Bulls Am. Paleont.* **11**(43), 140 pp.

Howell, B. F. 1937: Cambrian *Centropleura vermontensis* fauna of northwestern Vermont. *Bull. geol. Soc. Am.* **48**, 1147–1210.

Hubert, J. F., Suchecki, R. K. & Callahan, R. K. M. 1977: The Cow Head Breccia: sedimentology of the Cambro-Ordovician continental margin, Newfoundland. *In* Cook, H. E. & Enos, P. (ed.) Deep-water carbonate environments. *Spec. Publ. Soc. econ. Paleont. Mineral.* **25**, 125–154.

Hutchinson, R. D. 1952: Middle Cambrian of the Atlantic realm in eastern Gaspé. *Am. J. Sci.* **250**, 275–280.

Hutchinson, R. D. 1962: Cambrian stratigraphy and trilobite faunas of southeastern Newfoundland. *Bull. geol. Surv. Canada* **88**, 156 pp.

Ineson, J. R. 1980: Carbonate debris flows in the Cambrian of south-west Peary Land, eastern North Greenland. *Rapp. Grønlands geol. Unders.* **99**, 43–49.

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

Ineson, J. R., Surlyk, F., Higgins, A. K. & Peel, J. S. 1994: Slope apron and deep shelf sediments of the Brønlund Fjord and Tavsens Iskappe Groups (Lower Cambrian – Lower Ordovician) in North Greenland: stratigraphy, facies and depositional setting. *Bull. Grønlands geol. Unders.* **169** (this volume).

James, N. P. & Stevens, R. K. 1986: Stratigraphy and correlation of the Cambro-Ordovician Cow Head Group, western Newfoundland. *Bull. geol. Surv. Canada* **366**, 143 pp.

Jell, P. A. 1974: Faunal provinces and possible planetary reconstruction of the middle Cambrian. *J. Geol.* **82**, 319–350.

Jell, P. A. 1975: Australian Middle Cambrian eodiscoids with a review of the superfamily. *Palaeontographica* **A 150**, 1–97.

Kaesler, R. L. 1966: Quantitative re-evaluation of ecology and distribution of recent Foraminifera and Ostracoda of Todos Santos Bay, Baja California, Mexico. *Paleont. Contr. Univ. Kansas Pap.* **10**, 1–50.

Keppie, J. D. 1989: Northern Appalachian terranes and their accretionary history. *In* Dallmeyer, R. D. (ed.) Terranes in the circum-Atlantic orogens. *Spec. Pap. geol. soc. Am.* **230**, 159–192.

Kindle, C. H. 1982: The C. H. Kindle collection: Middle Cambrian to Lower Ordovician trilobites from the Cow Head Group, western Newfoundland. *Pap. geol. Surv. Can.* **82–1C**, 1–17.

Kruskal, J. B. 1964a: Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* **29**, 1–27.

Kruskal, J. B. 1964b: Nonmetric multidimensional scaling: a numerical method. *Psychometrica* **29**, 28–42.

Lochman-Balk, C. & Wilson, J. L. 1958: Cambrian biostratigraphy in North America. *J. Paleont.* **32**, 312–350.

Ludvigsen, R. 1978: Middle Ordovician trilobite biofacies, southern Mackenzie Mountains. *Spec. Pap. geol. Assoc. Can.* **18**, 1–37.

Maples, C. G. & Archer, A. W. 1988: Monte Carlo simulation of selected binomial similarity coefficients (II): effect of sparse data. *Palaios* **3**, 95–103.

McKerrow, W. S. & Cocks, L. R. M. 1976: Progressive faunal migration across the Iapetus Ocean. *Nature* **263**, 304–306.

McLaughlin, K. P. & Enbysk, B. B. 1950: Middle Cambrian trilobites from Pend Oreille County, Washington. *J. Paleont.* **24**, 466–471.

Menzies, R. J., George, R. Y. & Rowe, G. T. 1973: *Abyssal environment and ecology of the world oceans*, 488 pp. New York: Wiley-Interscience.

Nelson, C. A. 1963: Stratigraphic range of *Ogygopsis*. *J. Paleont.* **37**, 244–248.

Öpik, A. A. 1979: Middle Cambrian agnostids: systematics and biostratigraphy. *Bull. Bur. Miner. Resour. Austral.* **172**; vol. 1, 188 pp.; vol 2, 67 pls.

Palmer, A. R. 1969: Cambrian trilobite distributions in North America and their bearing on Cambrian paleogeography in Newfoundland. *In* Kay, M. (ed.) North Atlantic – geology and continental drift. *Mem. Am. Assoc. petrol. Geol.* **12**, 139–148.

Palmer, A. R. 1972: Problems of Cambrian biogeography. *Proc. 24 int. geol. Congr., Montreal* **7**, 310–315.

Palmer, A. R. 1973: Cambrian trilobites. *In* Hallam, A. (ed.) *Atlas of palaeogeography*, 3–11. Amsterdam: Elsevier.

Palmer, A. R. 1979: Cambrian. *In* Robison, R. A. & Teichert, C. (ed.) *Treatise on invertebrate paleontology,* part A, *biogeography and biostratigraphy*, A119–A135. Lawrence: Geol. Soc. Am. & Kansas Univ. Press.

Palmer, A. R. & Halley, R. B. 1979: Physical stratigraphy and trilobite biostratigraphy of the Carrara Formation (Lower and Middle Cambrian) in the southern Great Basin. *Prof. Pap. U.S. geol. Surv.* **1047**, 1–131.

Palmer, A. R. & Peel, J. S. 1981: Dresbachian trilobites and stratigraphy of the Cass Fjord Formation, western North Greenland. *Bull. Grønlands geol. Unders.* **141**, 46 pp.

Palmer, A. R. & Stewart, J. S. 1968: A paradoxidid trilobite from Nevada. *J. Paleont.* **42**, 177–179.

Peel, J. S. (ed.) 1988: Stratigraphy and palaeontology of the Holm Dal Formation (late Middle Cambrian), central North Greenland. *Meddr Grønland Geosci.* **20**, 168 pp.

Poulsen, C. 1927: The Cambrian, Ozarkian and Canadian faunas of northwest Greenland. *Meddr Grønland* **70**, 233–343.

Poulsen, C. 1960: Fossils from the late Middle Cambrian *Bolaspidella* Zone of Mendoza, Argentina. *Mat.-Fys. Medd. Danske Vid. Selsk.* **32**, 42 pp.

Poulsen, V. 1964: Contribution to the Lower and Middle Cambrian paleontology and stratigraphy of northwest Greenland. *Meddr Grønland* **164**(6), 105 pp.

Poulsen, V. 1969: An Atlantic Middle Cambrian fauna from North Greenland. *Lethaia* **2**, 1–14.

Poulsen, V. & Anderson, M. M. 1975: The Middle–Upper Cambrian transition in southeastern Newfoundland, Canada. *Can. J. Earth Sci.* **12**, 2065–2079.

Ramos, V. A., Jordan, T. E., Allmendinger, R. W., Mpodozis, C., Kay, S. M., Cortes, J. M. & Palma, A. 1986: Paleozoic terranes of the central Argentine–Chilean Andes. *Tectonics* **5**, 855–880.

Rasetti, F. 1951: Middle Cambrian stratigraphy and faunas of the Canadian Rocky Mountains. *Smithson. misc. Collns* **116** (5), 277 pp.

Rasetti, F. 1967: Lower and Middle Cambrian trilobite faunas from the Taconic sequence of New York. *Smithson. misc. Collns* **152**(4), 111 pp.

Robison, R. A. 1964: Late Middle Cambrian faunas from western Utah. *J. Paleont.* **38**, 510–566.

Robison, R. A. 1972: Mode of life of agnostid trilobites. *Proc. 24 int. geol. Congr., Montreal* **7**, 33–40.

Robison, R. A. 1976: Middle Cambrian trilobite biostratigraphy of the Great Basin. *Brigham Young Univ. geol. Stud.* **23**(2), 93–109.

Robison, R. A. 1984: Cambrian Agnostida of North America and Greenland, Part I, Ptychagnostidae. *Paleontol. Contr. Univ. Kansas Pap.* **109**, 59 pp.

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

Robison, R. A. 1991: Cambrian period. *In* Goetz, P. W. (ed.) *The new Encyclopaedia Brittanica*, 785–792. (15th edit.). Vol. 19. Macropaedia. Chicago.

Robison, R. A. 1994: Agnostoid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Bull. Grønlands geol. Unders.* **169** (this volume).

Robison, R. A. & Babcock, L. E. 1990: Biogeography of Middle Cambrian trilobites from North Greenland: implications for terrane analysis. *3 int. Symp. Cambrian System, Novosibirsk, USSR, Abstr.* 151.

Rushton, A. W. A. 1978: Fossils from the Middle–Upper Cambrian transition beds in the Nuneaton district. *Palaeontology* **21**, 245–283.

Samson, S., Palmer, A. R., Robison, R. A. & Secor, D. T., Jr. 1990: Biogeographical significance of Cambrian trilobites from the Carolina slate belt. *Bull. geol. Soc. Am.* **102**, 1459–1470.

Scotese, C. R. 1987: Phanerozoic plate tectonic reconstructions. *Paleoceanogr. map. Proj., Univ. Texas, Inst. Geophys., Tech. Rept* **40**, 54 pp.

Scotese, C. R., Bambach, R. K., Barton, C., Van der Voo, R. & Ziegler, A. M. 1979: Paleozoic base maps. *J. Geol.* **87**, 217–277.

Scotese, C. R. & Denham, C. R. 1988: *User's manual for Terra Mobilis: plate tectonics for the Macintosh,* 43 pp. Houston: Earth in Motion Technologies.

Scotese, C. R. & McKerrow, W. S. 1990: Revised world maps and introduction. *In* McKerrow, W. S. & Scotese, C. R. (ed.) Palaeozoic palaeogeography and biogeography. *Mem. geol. Soc. Lond.* **12**, 1–21.

Secor, D. T., Jr., Samson, S. L., Snoke, A. W. & Palmer, A. R. 1983: Confirmation of the Carolina slate belt as an exotic terrane. *Science* **221**, 649–650.

Shah, S. K. & Sudan, C. S. 1982: *Bolaspidella* from the Cambrian of Kashmir and its stratigraphic significance. *J. geol. Soc. India* **23**, 236–245.

Shaw, A. B. 1966: Paleontology of northwestern Vermont. XI. Fossils from the Middle Cambrian St. Albans Shale. *J. Paleont.* **40**, 843–858.

Shergold, J. H. 1988: Review of trilobite biofacies distributions at the Cambrian–Ordovician boundary. *Geol. Mag.* **125**, 363–380.

Skevington, D. 1974: Controls influencing the composition and distribution of Ordovician graptolite faunal provinces. *Spec. Pap. Palaeontology* **13**, 59–73.

Smith, A. G., Hurley, A. M. & Briden, J. C. 1981: *Phanerozoic paleocontinental world maps,* 102 pp. New York: Cambridge Univ. Press.

Sneath, P. H. A. & McKenzie, K. G. 1973: Statistical methods for the study of biogeography. *Spec. Pap. Palaeontology* **12**, 1–42.

Staff, G. M., Stanton, R. J., Jr., Powell, E. N. & Cummins, H. 1986: Time-averaging, taphonomy, and their impact on paleocommunity reconstruction: death assemblages in Texas bays. *Bull. geol. Soc. Am.* **97**, 428–443.

Stewart, J. H. & Palmer, A. R. 1967: Callaghan window – a newly discovered part of the Roberts thrust, Toiyabe Range, Lander County, Nevada. *Prof. Pap. U.S. geol. Surv.* **575D**, D56–D63.

Surlyk, F. 1991: Tectonostratigraphy of North Greenland. *Bull. Grønlands geol. Unders.* **160**, 25–47.

Sweet, W. C. & Bergström, S. M. 1974: Provincialism exhibited by Ordovician conodont faunas. *In* Ross, C. A. (ed.) Paleogeographic provinces and provinciality. *Soc. econ. Paleontol. Mineral. Spec. Publ.* **21**, 189–202.

SYSTAT, Inc. 1986: *SYSTAT: the system for statistics.*

Taylor, M. E. 1976: Indigenous and redeposited trilobites from Late Cambrian basinal environments of central Nevada. *J. Paleont.* **50**, 668–700.

Taylor, M. E. 1977: Late Cambrian of western North America: trilobite biofacies, environmental significance, and biostratigraphic implications. *In* Kauffman, E. G. & Hazel, J. E. (ed.) *Concepts and methods of biostratigraphy*, 397–425. Stroudsburg: Dowden, Hutchinson & Ross, Inc.

Taylor, M. E. & Cook, H. E. 1976: Continental shelf and slope facies in the Upper Cambrian and lowest Ordovician of Nevada. *Brigham Young Univ. geol. Stud.* **23**(2), 181–214.

Taylor, M. E. & Forester, R. M. 1979: Distributional model for marine isopod crustaceans and its bearing on early Paleozoic paleozoogeography and continental drift. *Bull. geol. Soc. Am.* **90**, 405–413.

Theokritoff, G. 1979: Early Cambrian provincialism and biogeographic boundaries in the North Atlantic region. *Lethaia* **12**, 281–295.

Theokritoff, G. 1985: Early Cambrian biogeography in the North Atlantic region. *Lethaia* **18**, 283–293.

Thomas, A. T., Owens, R. M. & Rushton, A. W. A. 1984: Trilobites in British stratigraphy. *Spec. Rept geol. Soc. Lond.* **16**, 78 pp.

Torsvik, T. H., Ryan, P. D., Trench, A. & Harper, D. A. T. 1991: Cambrian–Ordovician paleogeography of Baltica. *Geology* **19**, 7–10.

Ulrich, E. O. & Schuchert, C. 1902: Paleozoic seas and barriers in eastern North America. *Bull. N.Y. State Mus.* **52**, 633–663.

Valentine, J. W. 1973: *Evolutionary paleoecology of the marine biosphere,* 511 pp. New Jersey: Prentice-Hall.

Westergård, A. H. 1946: Agnostidea of the Middle Cambrian of Sweden. *Sver. geol. Unders.* **C 477**, 141 pp.

Westergård, A. H. 1953: Non-agnostidean trilobites of the Middle Cambrian of Sweden III. *Sver. geol. Unders.* **C 526**, 59 pp.

Williams, H. & Hatcher, R. D., Jr. 1982: Suspect terranes and accretionary history of the Appalachian orogen. *Geology* **10**, 530–536.

Wilson, J. T. 1966: Did the Atlantic close and then reopen? *Nature* **211**, 676–681.

Young, G. A. & Ludvigsen, R. 1989: Mid-Cambrian trilobites from the lowest part of the Cow Head Group, western Newfoundland. *Bull. geol. Surv. Can.* **392**, 49 pp.

Young, G. C. 1986: Cladistic methods in Paleozoic reconstruction. *J. Geol.* **94**, 523–537.

An enigmatic cap-shaped fossil from the Middle Cambrian of North Greenland

John S. Peel

Nyeboeconus robisoni gen. et sp. nov., is described from the Middle Cambrian Henson Gletscher Formation of western North Greenland. Some authors have interpreted similar shells as chondrophorine hydrozoans or invertebrate fossils of uncertain systematic position. The coiled, cap-shaped shell and the presence of an internal plate, or pegma, suggest, however, that this new form is the second genus to be described of the Family Enigmaconidae MacKinnon, 1985 (Mollusca, Class Helcionelloida), otherwise known only from rocks of similar age in New Zealand.

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Lower and Middle Cambrian strata yield a variety of mainly small cap-shaped shells which are not readily assigned to molluscan classes, such as the Gastropoda or Tergomya, living at the present day (Peel, 1991a, b). Notable amongst these small fossils are shells of the Class Helcionelloida which are characterised by a bilaterally symmetrical (isostrophic) cap-shaped form, usually coiled through less than one whorl (Peel, 1991b).

Helcionelloids are widespread and diverse (e.g. Rozanov *et al.*, 1969 (= Raaben, 1981); Runnegar & Jell, 1976; MacKinnon, 1985; Geyer, 1986; Yu, 1987; Peel, 1988, 1991b; Missarzhevsky, 1989; Bengtson *et al.*, 1990; Benton & Erwin, 1993) but their record in post-Middle Cambrian strata is uncertain, as is their relationship to the molluscan groups which survive them.

Reconstruction of helcionelloid anatomy is not without dispute; helcionelloids have been considered to be gastropods (i.e., torted molluscs) but at the present day there is general agreement that they were untorted. In a model strongly influenced by a search for the origin of the Bivalvia, Runnegar & Pojeta (1974; see also Pojeta & Runnegar, 1976; Runnegar & Pojeta, 1985) considered helcionelloids to be exogastrically coiled untorted molluscs (i.e., with the apex lying anteriorly) similar to tryblidiid Tergomya such as *Pilina, Tryblidium* and the extant *Neopilina*. Others have interpreted the apex in helcionelloids to lie at the posterior such that coiling of the shell is endogastric (Yochelson, 1978, 1979; Geyer, 1986; Peel & Yochelson, 1987; Peel, 1988, 1991a, b). Peel (1991a, b) asserted this view in formally separating the endogastric helcionelloids from the exogastric Tergomya; both helcionelloids and tergomyans were regarded as untorted.

The contrasting reconstructions of helcionelloids both rely heavily on interpretations of the mantle cavity, in particular the pattern of presumed inhalant and exhalant respiratory water currents. Taking into account the general small size of most helcionelloids (cf. Runnegar & Jell, 1976; Runnegar & Pojeta, 1985), it can not be assumed that these interpretations are valid. Most of the minute helcionelloids were subject to different physical and biomechanical constraints than the significantly larger molluscs which formed the basis for the mantle cavity reconstructions. While refuting the exogastric reconstruction of helcionelloids proposed by Runnegar & Pojeta (1974), Peel (1991b, pp. 19–20) admitted that his preferred endogastric model accepted the same precept that water transport into and out of the helcionelloid shell was possible.

The cap-shaped shell form is not restricted to the Helcionelloida in the Lower and Middle Cambrian. Articulated halkieriids (Conway Morris & Peel, 1990; Peel, 1991c) from the Lower Cambrian of North Greenland preserve a calcareous cap- shaped shell at the anterior and posterior extremities and the latter, in particular, is not unlike some molluscan shells in gross form. A broadly similar spectrum of shell forms of problematic origin has been documented by Qian & Bengtson (1989) from the earliest Cambrian of China, demonstrating that a variety of organisms produced shells of this type. That such a morphology is not necessarily indicative of molluscan affinity is clearly demonstrated by suggestions that some

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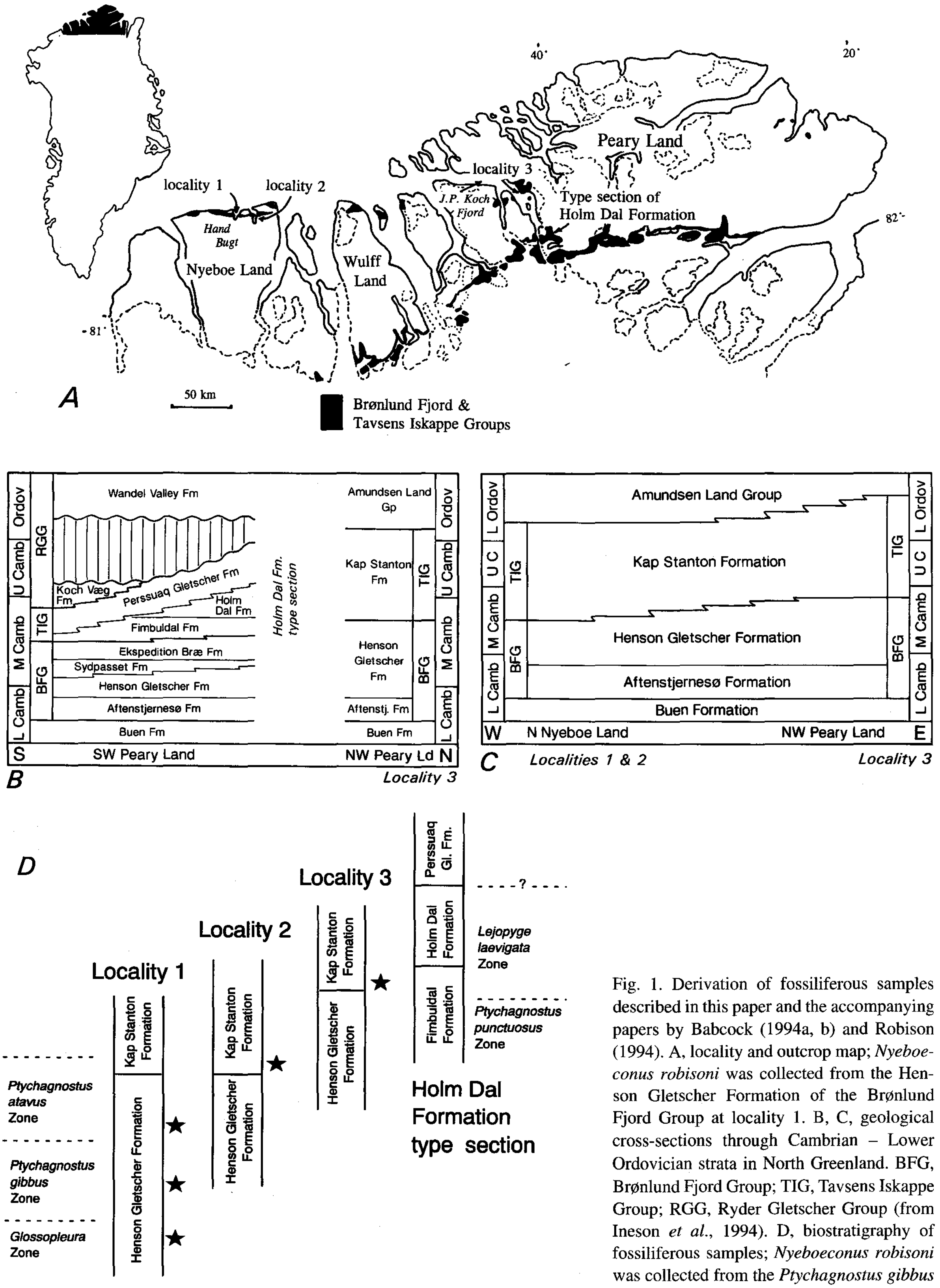

Fig. 1. Derivation of fossiliferous samples described in this paper and the accompanying papers by Babcock (1994a, b) and Robison (1994). A, locality and outcrop map; *Nyeboeconus robisoni* was collected from the Henson Gletscher Formation of the Brønlund Fjord Group at locality 1. B, C, geological cross-sections through Cambrian – Lower Ordovician strata in North Greenland. BFG, Brønlund Fjord Group; TIG, Tavsens Iskappe Group; RGG, Ryder Gletscher Group (from Ineson *et al.*, 1994). D, biostratigraphy of fossiliferous samples; *Nyeboeconus robisoni* was collected from the *Ptychagnostus gibbus* interval-zone at locality 1.

of these Cambrian fossils may represent chondrophorine hydrozoans (Yochelson & Gil Cid, 1984; Stanley, 1986; Babcock & Robison, 1988). Thus, the cap-shaped fossil in these forms is no longer interpreted by these authors as the external, calcareous, dorsal shell of a mollusc, but as an impression of the internal, organic, float (pneumatophore) of a medusoid cnidarian.

A single enigmatic fossil of Middle Cambrian age from the Henson Gletscher Formation of northern Nyeboe Land promotes a discussion of these possible interpretations, also the suggestion by Evans (1992) that similar fossils may represent an invertebrate of presently unknown affinity. The specimen is associated with a few non-trilobite fossils which were kindly brought to my attention by Richard A. Robison; it is described below as *Nyeboeconus robisoni* gen. et sp. nov. in his honour, in gratitude for his studies and advice concerning Greenland Cambrian fossils during the past decade.

Nyeboeconus robisoni is from the Henson Gletscher Formation, west of Hand Bugt, northern Nyeboe Land, western North Greenland (Fig. 1, locality 1). Several specimens of the helcionelloid *Latouchella* are also present in the same sample (GGU 298970), associated with elkaniid, acrotretid and orthoid brachiopods (Lars E. Holmer, personal communication, 1993), conodontomorphs and the mollusc *Pelagiella*. Pelagiellids also form a characteristic group of molluscs in Lower and Middle Cambrian strata. While possibly related to helcionelloids, they are readily distinguished by anisostrophic coiling which gives a superficial resemblance to the gastropod shell.

The most conspicuous fossils in the Henson Gletscher Formation at the collection locality are polymeroid and agnostoid trilobites described elsewhere in this volume by Babcock (1994a, b) and Robison (1994). An accompanying paper by Ineson *et al.* (1994) provides a stratigraphic and environmental background for these faunal descriptions.

Systematic description

Genus *Nyeboeconus* gen. nov.

Type species. Nyeboeconus robisoni gen. et sp. nov.

Derivation of name. From Nyeboe Land, North Greenland and *conus* (latin), a cone.

Diagnosis. Cap-shaped fossil, slightly elongate in the plane of bilateral symmetry, in plan view; coiled through about one quarter of a revolution, with clearly distinguished sub-apical and supra-apical surfaces and a sub-central apex. Internal mould with prominent comarginal rugae on the supra-apical surface, crossed by sharply defined radial grooves and varices; a prominent transverse groove on the internal mould represents a plate (pegma) on the sub-apical surface of the shell interior. Shell calcareous and seemingly thin, with an external ornamentation of radial ridges which correspond in their position to the grooves on the internal mould.

Discussion. In terms of the prominent pegma on the shell interior, *Nyeboeconus* closely resembles *Enigmaconus* MacKinnon, 1985 (Class Helcionelloida) from the late Middle Cambrian of New Zealand (MacKinnon, 1985, pp. 72–74, fig. 7). It is readily distinguished from this genus by its prominent ornamentation of rugae and radial grooves on the internal mould and less laterally compressed form; the internal mould (and consequently the shell interior) in *Enigmaconus* is smooth. The shell in *Enigmaconus* also appears to be taller, but this (together with some of the lateral compression) may in part reflect preservation of just the early part of the New Zealand shell as an internal mould; this is supported by comparison of *Enigmaconus* and *Nyeboeconus* in lateral aspect. In the former (cf. MacKinnon, 1985, fig. 7b, n), the most abapical part of the slot representing the pegma lies much closer to the latest preserved apertural margin than the corresponding point in *Nyeboeconus* (Fig. 2b).

The general similarity of *Nyeboeconus* to *Enigmaconus* in terms of shell form and the pegma warrants placement of the Greenland form within the Family Enigmaconidae MacKinnon, 1985. It should be noted that MacKinnon (1985, p. 72) considered the pegma to lie nearest to the shell anterior while this surface is here interpreted as posterior (cf. Peel, 1991a, b).

In terms of the unusual ornamentation of the inner surface of the shell, *Nyeboeconus* resembles *Marocella* Geyer, 1986 of uncertain systematic position which was proposed on the basis of specimens from the Cambrian of Morocco. Geyer (1986) assigned to this genus specimens described as *Scenella morenensis* sp. nov. by Yochelson & Gil Cid (1984) from the Cambrian of Spain, and interpreted as the floats of chondrophorine hydrozoans. *Nyeoboeconus* differs from these specimens, and from additional material of *Marocella* described from Antarctica by Evans (1992), in possessing a prominent transverse pegma on the shell interior.

At first glance, *Nyeboeconus* bears some resemblance to the reconstruction (in dorsal aspect) presented by Conway Morris *et al.* (1991) of the problematic organism *Libodiscus ascitus* from the Upper Palaeozoic of Canada, showing a disc with concentric markings and some sort of transverse structure. The similarity, however, is quite superficial, although relevant in this context on account of the comparison between *Libodiscus* and supposed chondrophorines made by Conway Morris *et al.* (1991).

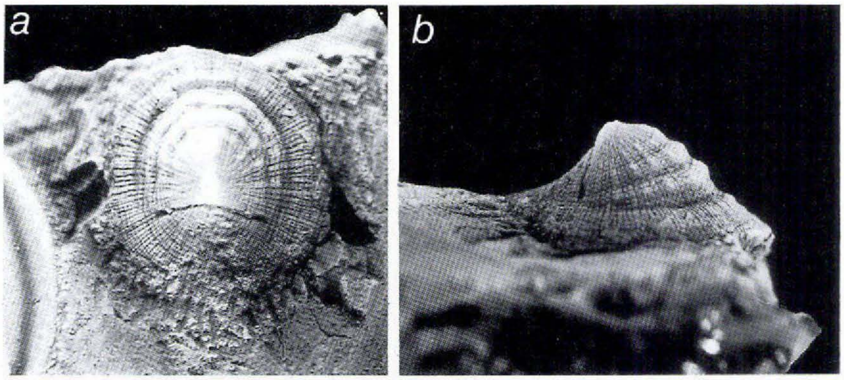

Fig. 2. *Nyeboeconus robisoni* gen. et sp. nov. MGUH 22.188 from GGU sample 298970, Henson Gletscher Formation, northern Nyeboe Land, western North Greenland (Fig. 1), internal mould, × 5 (photo: R. A. Robison). a, apical view showing prominent comarginal rugae, radial ornamentation and the transverse groove representing the pegma. Fragments of shell with external ornamentation of radial ribs and growth lines occur on the supra-apical surface (top left) and around the apertural margins. b, lateral view showing the concave sub-apical surface (left) with pegma and the convex supra-apical surface with conspicuous comarginal rugae. Note the slightly protuberant apex which is slightly broken and the strong radial ornamentation.

Nyeboeconus robisoni gen. et sp. nov.

Fig. 2

Holotype. MGUH 22.188 from GGU sample 298970, Henson Gletscher Formation, northern Nyeboe Land, western North Greenland (Fig. 1, locality 1). GGU sample 298970 was collected at a height of 102 m in the section through the Aftenstjernesø, Henson Gletscher and Kap Stanton Formations at Hand Bugt (cf. Ineson *et al.*, 1994, fig. 4b and Babcock, 1994a, fig. 2). The specimen is preserved on the same small slab as a cephalon of *Lejopyge barrandei* (MGUH 21.416) illustrated by Robison (1994, fig. 23.1a, b).

Description. The only known specimen of this species is a cap-shaped fossil which, in dorsal view, is slightly longer in the plane of bilateral symmetry than wide; the apex is slightly excentric, lying closer to the apertural margin on the sub-apical surface. In lateral aspect, the shell is clearly coiled through about one quarter of a whorl, with a convex supra-apical surface and a concave sub-apical surface; shell height is almost two-thirds of shell length. Apex slightly protuberant on the internal mould, smooth. The dorsal surface carries strongly developed comarginal rugae which are most conspicuous on the supra-apical surface, but fade away across the lateral areas as the sub-apical surface is approached. These are crossed by closely spaced and sharply defined radiating grooves on the internal mould, presumably corresponding to sharp ridges on the shell interior; series of elongate radial nodes, or varices, cross the convex surfaces of the rugae on the supra-apical surface. In the final preserved growth stage, comarginal rugae are absent and the planar aperture is slightly expanded.

A deep slot is present on the internal mould on the sub-apical surface, representing a plate (pegma) extending into the shell interior. The groove terminates near the base of the final prominent ruga on each lateral area; the bottom of the groove slopes up (adapically) from each lateral area towards the median plane of symmetry. Thus, the adapical surface of the pegma was probably arched and not a simple plate extending transversely straight across the shell interior from the lowest point of the groove on one side to the corresponding position on the other side.

Fragments on the supra-apical surface and near the apertural margin indicate that the shell is calcareous and thin; radiating spiral ridges on the shell exterior correspond in position to the radiating grooves on the internal mould.

Discussion. On account of the prominent ornamentation, casual examination suggests that the single specimen preserves the shell exterior and that this surface is ornamented with radiating cords separated by narrow grooves (Fig. 2). Closer scrutiny reveals, however, fragments of calcareous shell on the supra-apical surface with raised radial ribs and growth lines. The deep transverse slot largely filled with calcareous shell material, representing the pegma, also serves to confirm that this is an internal mould. Thus, the shell interior carries radial ridges which are reflected on the internal mould as deep grooves; the thinness of the preserved shell fragments indicates that the coarse comarginal rugae affected both the outer and inner shell surfaces.

In view of the very small size of the preserved shell fragments it is difficult to assess if any exfoliation of shell material has taken place during separation of the fossil from the matrix. It remains possible, therefore, that the original shell thickness was somewhat greater than that preserved. The presence of clearly discernible radial ornamentation on the fragments of shell argues strongly that the calcareous shell material is not a secondary calcareous deposit.

Stratigraphic age. The only known specimen of *Nyeboeconus robisoni* is from the Henson Gletscher Formation at Hand Bugt, northern Nyeboe Land, western North Greenland (Fig. 1, locality 1). Agnostoid trilobites from the same collection (GGU 298970) are interpreted as belonging to the upper part of the *Ptychagnostus gibbus* interval-zone of the Middle Cambrian in an accompanying paper in this volume by Robison (1994). Co-occurring polymeroid trilobites are described in papers in this volume by Babcock (1994a, b). In the same section, the Henson Gletscher Formation ranges up into the *Ptychagnostus atavus* interval-zone of the Middle Cambrian, and possibly also to the latest Middle Cambrian at locality 3 (Fig. 1). In more southern outcrops in North Greenland, along the margin of the Inland Ice, the formation is mainly of Early Cambrian age (Higgins *et al.*, 1991a, b; Ineson *et al.*, 1994).

Chondrophore or mollusc?

In proposing *Marocella* as a mollusc-like shell of uncertain affinity, Geyer (1986) clearly indicated that this form is distinct from *Scenella* which he regarded as a tryblidiid monoplacophoran (= tergomyan of current usage, although the genus is now considered to be a helcionelloid, cf. Peel, 1991a, b,). Thus, the assignment of *Scenella* to the chondrophorine hydrozoans proposed by Yochelson & Gil Cid (1984) was refuted, an opinion also reiterated by Berg-Madsen & Peel (1986) and Landing & Narbonne (1992). The interior of the calcareous shell in *Scenella* is smooth, lacking the deep grooves seen in *Marocella* and *Nyeboeconus*.

Yochelson & Gil Cid (1984; see also Stanley, 1986) are probably correct in their assertion that many Cambrian and Ordovician fossils identified in collections or in the literature as *Scenella* may be chondrophores, but their extension of this concept to the type materials of *Scenella* as illustrated by Knight (1941) is inappropriate. Relevant non-chondrophorine features of these type specimens include the calcareous shell and the distinct spiral coiling.

The detailed description of *Marocella* by Evans (1992) demonstrates that the structure and ornamentation of the shell interior is seemingly without parallel in molluscs. In particular, the sharp ridges on the shell interior can not be reconciled with the normally smooth (or smoothened) internal surface of molluscan cap-shaped shells. There is some similarity in terms of ornamentation with the non-calcareous, internal float of the extant chondrophore *Porpita* which attains a size of up to 8 cm in diameter (Stanley, 1986), more than 10 times larger than *Marocella*. The float of *Porpita* is not coiled, however, and it is radially symmetrical about the central apex, whereas *Marocella* is clearly coiled with distinct sub-apical and supra-apical surfaces.

In terms of coiling, *Marocella* resembles *Nyeboeconus* but the general similarity in terms of ornamentation on the inner surface is less marked in detail. The latter genus has broad comarginal rugae and not the sharply defined rugae seen in *Marocella*; the spiral rugae of *Marocella* have not been discerned in *Nyeboeconus*.

Evans (1992) noted that shells of *Marocella* showed some similarity to the terminal plates of halkieriids (cf. Conway Morris & Peel, 1990; Peel, 1991c) but preferred to leave the affinity of the genus unresolved. The comparison of *Marocella* to the halkieriid shells may prove to be an attractive general model for future reconstructions but available data can not yet add further substantiation.

On balance, the calcareous shell and shell coiling of *Nyeboeconus* suggest that this genus is a mollusc and not a chondrophorine hydrozoan, although the ornamentation of the shell interior remains problematic. The high degree of similarity with *Enigmaconus* in terms of the sub-apical pegma is perhaps the most convincing indicator of molluscan affinities. Pojeta (1985) regarded the appearance of a pegma to be the delimiting character of the Class Rostroconchia from its helcionelloid ancestor, although Peel (1991a,b) has demonstrated that pegma-like structures are developed in a variety of helcionelloids. However, the pegma of *Nyeboeconus* compares well with the same structure in rostroconchs (cf. Pojeta & Runnegar, 1976), adding impetus to the suggestion of MacKinnon (1985) that *Enigmaconus* (and now *Nyeboeconus*) might be suitable ancestral forms to the Rostroconchia.

To summarise, while a possible Cambrian record for chondrophorine hydrozoans is acknowledged, *Scenella* and *Nyeboeconus* are considered to be helcionelloid molluscs, although the internal ornamentation of the latter genus is admittedly unusual. *Marocella* is not placed systematically, in agreement with Geyer (1986) and Evans (1992).

Acknowledgements. GGU indicates samples collected by the Geological Survey of Greenland (Grønlands Geologiske Undersøgelse);

MGUH denotes the type collection of the Geological Museum, Copenhagen. I am grateful to Lars Holmer and Sören Jensen (Uppsala University) for reviewing the manuscript.

References

Babcock, L. E. 1994a: Systematics and phylogenetics of polymeroid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Bull. Grønlands geol. Unders.* **169** (this volume).

Babcock, L. E. 1994b: Biogeography and biofacies patterns of Middle Cambrian polymeroid trilobites from North Greenland: palaeogeographic and palaeo-oceanographic implications. *Bull. Grønlands geol. Unders.* **169** (this volume).

Babcock, L. E. & Robison, R. A. 1988: Taxonomy and paleobiology of some Middle Cambrian *Scenella* (Cnidaria) and hyolithids (Mollusca) from western North America. *Paleont. contr. Univ. Kansas Pap.* **121**, 22 pp.

Bengtson, S., Conway Morris, S., Cooper, B. J., Jell, P. A. & Runnegar, B. N. 1990: Early Cambrian fossils from South Australia. *Mem. Australas. Assoc. Palaeontol.* **9**, 364 pp.

Benton, M. J. & Erwin, D. H. 1993: Mollusca: Amphineura and 'Monoplacophora' *In* Benton, M. J. (ed.) *The fossil record 2*, 125–130.

Berg-Madsen, V. & Peel, J. S. 1986: *Scenella barrandei* (Mollusca) from the Middle Cambrian of Baltoscandia. *Norsk geol. Tidsskr.* **66**, 81–86.

Conway Morris S. & Peel, J. S. 1990a: Articulated halkieriids from the Lower Cambrian of north Greenland. *Nature* **345** (6278), 802–805.

Conway Morris, S., Savoy, L. E. & Harris, A. G. 1991: An enigmatic organism from the 'Ekshaw' Formation (Devonian–Carboniferous), Alberta, Canada. *Lethaia* **24**, 139–152.

Evans, K. R. 11992: *Marocella*: Antarctic specimens of an enigmatic Cambrian animal. *J. Paleont.* **66**, 558–562.

Geyer, G. 1986: Mittelkambrische Mollusken aus Marokko und Spanien. *Senckenbergiana lethaea* **67**, 55–118.

Higgins, A. K., Ineson, J. R., Peel, J. S. Surlyk, F. & Sønderholm, M. 1991a: Lower Palaeozoic Franklinian Basin of North Greenland. *Bull. Grønlands geol. Unders.* **160,** 71–139.

Higgins, A. K., Ineson, J. R., Peel, J. S. Surlyk, F. & Sønderholm, M. 1991b [issued 1992]: Cambrian to Silurian basin development and sedimentation, North Greenland. *In* Trettin, H. P. (ed.) *Geology of the Innuitian orogen and arctic platform of Canada and Greenland,* 111–161. *Geology of Canada* **3**. (Also *The geology of North America* **E**.) Ottawa: Geological Survey of Canada.

Ineson, J. R., Surlyk, F., Higgins, A. K. & Peel, J. S. 1994: Slope apron and deep shelf sediments of the Brønlund Fjord and Tavsens Iskappe Groups (Lower Cambrian – Lower Ordovician) in North Greenland: stratigraphy, facies and depositional setting. *Bull. Grønlands geol. Unders.* **169** (this volume).

Knight, J. B. 1941: Paleozoic gastropod genotypes. *Spec. Pap. geol. Soc. Am.* **32**, 425 pp.

Landing, E. & Narbonne, G. M. 1992: *Scenella* and A chondrophorine (medusoid hydrozoan) from the basal Cambrian (Placentian) of Newfoundland. *J. Paleont.* **66**, 338 only.

MacKinnon, D. I. 1985: New Zealand late Middle Cambrian molluscs and the origin of Rostroconchia and Bivalvia. *Alcheringa* **9**, 65–81.

Missarzhevsky, V. V. 1989: [Oldest skeletal fossils and stratigraphy of Precambrian and Cambrian boundary beds]. *Trudy Ordena Trydov. Kras. Zhameni geol. Inst. Akad. Nauk SSSR* **443**, 237 pp. [in Russian].

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

Peel, J. S. 1991a: Functional morphology of the Class Helcionelloida nov., and the early evolution of the Mollusca. *In* Simonetta, A. & Conway Morris, S. (ed.) *The early evolution of Metazoa and the significance of problematic taxa*, 157–177. Cambridge: Cambridge Univ. Press and Univ. Camerino.

Peel, J. S. 1991b: The Classes Tergomya and Helcionelloida, and early molluscan evolution. *Bull. Grønlands geol. Unders.* **161**, 11–65.

Peel, J. S. 1991c: Introduction – articulated halkieriids and microchitons. *Bull. Grønlands geol. Unders.* **161**, 5–10.

Peel, J. S. & Yochelson, E. L. 1987: New information on *Oelandia* (Mollusca) from the Middle Cambrian of Sweden. *Bull. geol. Soc. Denmark* **36**, 263–273.

Pojeta, J., Jr. & Runnegar, B. 1976: The paleontology of rostroconch molluscs and the early history of the Phylum Mollusca. *[U. S.] geol. Surv. Prof. Pap.* **968**, 88 pp.

Pojeta, J. Jr. & Runnegar, B. 1985: The early evolution of diasome molluscs. *In* Trueman, E. R. & Clarke, M. R. (ed.) *The Mollusca* **10,** *Evolution*, 295–336. Orlando: Academic Press.

Qian Yi & Bengtson, S. 1989: Palaeontology and biostratigraphy of the Early Cambrian Meishucunian Stage in Yunnan Province, South China. *Fossils and Strata* **24**, 156 pp.

Raaben, M. E. (ed.) 1981: The Tommotian Stage and the Cambrian lower boundary problem. New Delhi: Amerind Publ. Co., 359 pp. [English translation of Rozanov *et al.*, 1969].

Robison, R. A. 1994: Agnostoid trilobites from the Henson Gletscher and Kap Stanton formations (Middle Cambrian), North Greenland. *Bull. Grønlands geol. Unders.* **169** (this volume).

Rozanov, A. Yu., Missarzhevsky, V. V., Volkova, N. A., Voronova, L. G., Krylov, I. N., Keller, B. M., Korolyuk, I. K., Lendzion, K., Michniak, R., Pykhova, N. G. & Sidorov, A. D. 1969: [The Tommotian Stage and the problem of the lower boundary of the Cambrian]. *Trudy Geologicheskogo Inst. Akad. Nauk SSSR* **296**, 380 pp. [in Russian., see Raaben (1981) for English translation].

Runnegar, B. & Jell, P. A. 1976: Australian Middle Cambrian molluscs and their bearing on early molluscan evolution. *Alcheringa* **1**, 109–138.

Runnegar, B. & Jell, P. A. 1980: Australian Middle Cambrian molluscs: corrections and additions. *Alcheringa* **4**, 111–113.

Runnegar, B. & Pojeta, J., Jr. 1974: Molluscan phylogeny: the paleontological viewpoint. *Science* **186**, 311–317.

Runnegar, B. & Pojeta, J., Jr. 1985: Origin and diversification of the Mollusca. *In* Trueman, E. R. & Clarke, M. R. (ed.) *The Mollusca* **10,** *Evolution*, 1–57. Orlando: Academic Press.

Stanley, G. D. 1986: Chondrophorine hydrozoans as problematic fossils. *In* Hoffman, A. & Nitecki, M. H. (ed.) *Problematic fossil taxa*, 68–86. New York: Oxford Univ. Press.

Yochelson, E. L. 1978: An alternative approach to the interpretation of the phylogeny of ancient mollusks. *Malacologia* **17**, 165–191.

Yochelson, E. L. 1979: Early radiation of Mollusca and mollusc-like groups. *In* House, M. R. (ed.) *The origin of the major invertebrate groups*, 323–358. New York: Academic Press.

Yochelson, E. L. & Gil Cid, M. D. 1984: Reevaluation of the systematic position of *Scenella. Lethaia* **17**, 331–340.

Yu Wen 1987: Yangtze micromolluscan fauna in Yangtze Region of China, with notes on Precambrian–Cambrian boundary. *Stratigraphy and palaeontology of systematic boundaries in China. Precambrian–Cambrian Boundary (1)*, 19–344. Nanjing: Nanjing Univ. Publ. House.

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