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Lower Cambrian trilobites from North Greenland

Mark R. Blaker and John S. Peel



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MEDDELELSER OM GRØNLAND, GEOSCIENCE 35 · 1997

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S. Funder, Geological Museum, Øster Voldgade 5-7, DK-1350 Copenhagen K, Denmark. Telephone +45 35 32 23 63. Telefax +45 35 32 23 25. E-mail: SBF@ savik.geomus.ku.dk.

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Lower Cambrian trilobites from North Greenland

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Fifty five trilobite species are described from Lower Cambrian platform margin to outer shelf deposits of North Greenland. The species indicate the "Nevadella" and Olenellus Zones of the North American standard, equivalent to uppermost Atdabanian(?), Botomian and Toyonian of Siberian usage. Basal siliciclastic sediments of the Buen Formation yield a Buenellus higginsi fauna ("Nevadella" Zone), including the exceptionally preserved fossils of the Sirius Passet fauna. A Linniphacos perspicultum and Olenellus hyperboreus fauna indicates the "Nevadella" and Olenellus zonal boundary while uppermost beds contain O. svalbardensis and Alacephalus? davisi (Olenellus Zone). Carbonate and siliciclastic sediments of the overlying Brønlund Fjord Group yield trilobites of the upper Olenellus Zone. The Kap Troedsson and Aftenstjernesø Formations contain Ekwipagetia marginata, Serrodiscus spp. and Calodiscus lobatus. Species of Kootenia, Ogygopsis, Zacanthopsis, Perissopyge, Pagetides and Bonnia are conspicuous from the Henson Gletscher Formation, together with Peronopsis roddvi. Oryctocephalids such as Arthricocephalus chauveaui and Halikoplanktos jishouensis allow correlation with the Megapalaeolenus Zone of China and are also recognised in Siberia. The Sæterdal Formation contains olenelloids, Kootenia marcoui, and Bonnia brennus. New genera: Limniphacos, Haliplanktos. New species: Limniphacos perspicullum, Kootenia oscari, K. radiata, K. sagena.

Key words. - Lower Cambrian, trilobites. North Greenland, systematics, biostratigraphy, intercontinental correlation.

Mark R. Blaker, Department of Geology, The University, Keele, Staffs ST5 5BG, U. K.; John S. Peel, Department of Historical Geology & Palaeontology, Institute of Earth Sciences, Uppsala University, Norbyvägen 22, S-752 36 Uppsala, Sweden (address for correspondence).

Introduction

From a historical perspective, the Cambrian of the northern coast of Greenland is best known from Inglefield Land, in North-West Greenland (Fig. 1), where platform interior deposits now referred to the Ryder Gletscher Group yielded rich faunas during early exploration (Koch 1925; Poulsen 1927, 1958a, 1964; Troelsen 1950; Cowie 1961, 1971; Dawes 1976). Recent work in this region and in the Washington Land area is reported by Henriksen & Peel (1976), Palmer & Peel (1981), Peel & Christie (1982), Bergström & Peel (1988) and Higgins *et al.* (1991a, b).

Information concerning the Cambrian in North Greenland, further to the east, is mainly of more recent origin and stems largely from regional geological investigations conducted by the Geological Survey of Greenland between 1978 and 1985 during the two phases of its North Greenland Project (Henriksen & Higgins 1991). Most Cambrian faunas collected during this project were derived from shelf deposits referred to the Buen Formation and the overlying Brønlund Fjord Group and Tavsens Iskappe Group (Fig. 2). Principal studies of the Cambrian arising from the North Greenland Project include Ineson (1985), Ineson & Peel (1980, 1987, 1997), Peel (1988a, 1994a) and Peel & Sønderholm (1991). Earlier contributions include Troelsen (1949, 1956), Jepsen (1971), Peel *et al.* (1974), Poulsen (1974), Christie & Peel (1977) and Palmer & Peel (1979).

Exceptionally preserved Lower Cambrian fossils from the Buen Formation at Sirius Passet, north-west Peary Land (Fig. 3, locality 5), were described by Budd (1993, 1995), Conway Morris *et al.* (1987) and Conway Morris & Peel (1990, 1995); see also Rigby (1986) and Blaker (1988).

The Lower Cambrian trilobite faunas of North Greenland have previously not been the subject of comprehensive study although Poulsen (1974) and Blaker (1988) have described three olenelloids from Peary Land. Middle Cambrian faunas were studied by Poulsen (1969), Palmer & Peel (1981), Robison (1982, 1984, 1988, 1994), Hood & Robison (1988) and Babcock (1994a, b). In contrast, Lower and Middle Cambrian trilobite faunas from Inglefield Land in North-West Greenland have received more detailed attention (Poulsen 1927, 1958a, 1964). Upper Cambrian trilobites (Dresbachian-Trempealeauan) are known from southern Washington Land (= Daugaard-Jensen Land) in western North Greenland but are only partially described (Palmer & Peel 1979, 1981). Cambrian strata are also well-known in North-East Greenland (Cowie & Adams 1957; Cowie 1971; Peel 1982; Pickerill & Peel 1990) and Lower Cambrian faunas were described by Poulsen (1932).





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graphical map shows localities in southern Peary Land along Wandel Dal This bulletin presents descriptions of 55 species of Lower Cambrian trilobites from North Greenland mainly collected during the North Greenland Project (1978-1985). The trilobites comprise one of the most diverse faunas recognised from the late Early Cambrian (mainly *Olenellus* Zone) and are of particular interest in furthering correlation between Laurentia and other Cambrian continents.

Geological setting

General reviews of the Lower Palaeozoic geology of North Greenland were given by Dawes (1976), Dawes & Peel (1981), Peel (1982) and Higgins *et al.* (1991a, b). Peel & Sønderholm (1991) presented an extensive review of North Greenland sedimentary basins. The following summary is derived from a comprehensive description of the Cambrian shelf stratigraphy of North Greenland by Ineson & Peel (1997; see also Peel 1988a, 1994a) which forms the stratigraphic basis for the present description of Lower Cambrian trilobite faunas.

The Lower Palaeozoic of North and North-West Greenland is composed of sedimentary rocks which were deposited principally in shallow-water carbonate platform, shelf and deep-water trough environments, representing the eastern continuation of the Franklinian Basin succession of the Canadian Arctic Islands (Trettin 1991; Higgins et al. 1991a, b). Extensive outcrops occur from Inglefield Land in the west to Danmark Fjord in the east in a belt measuring almost 1000 km east-west and about 200 km north-south (Figs 1, 2). The Franklinian Basin succession in Greenland includes some 8 km of Cambrian, Ordovician and Silurian sedimentary rocks and embraces a southern shelf succession, with a general northerly dip, and a northern deep-water trough succession. The northern limit of the deep-water trough has not been recognised in Greenland (Higgins et al. 1991a, b; Surlyk 1991).

Deposition within the Franklinian Basin in Greenland was brought to an end by the Ellesmerian Orogeny during the middle Palaeozoic. This deformation produced the east-west trending North Greenland fold belt which was largely restricted to the deep-water trough. Carboniferous and younger strata unconformably overlie the Franklinian Basin succession in eastern and northern areas of North Greenland (Fig. 1; Stemmerik & Håkansson 1991; Håkansson *et al.* 1991).

The Cambrian shelf succession overlies Precambrian crystalline basement in Inglefield Land (Peel *et al.* 1982) and possibly at the head of Victoria Fjord. Cambrian shelf deposits unconformably overlie Proterozoic sedimentary successions in southern Inglefield Land and the area east of Victoria Fjord (Dawes *et al.* 1982; Peel *et al.* 1982; Sønderholm & Jepsen 1991; Surlyk 1991). The base of the Franklinian Basin succession is not seen in the northern deep-water succession and late Proterozoic

sedimentary rocks may be present beneath Cambrian outcrops.

The Cambrian is conformably overlain by Ordovician strata within the deep-water trough succession and in western outcrops of the shelf succession. In areas to the east of Nordenskiöld Fjord the Cambrian succession is unconformably overlain by upper Lower Ordovician carbonate sediments of the Wandel Valley Formation (Figs 1, 2). These carbonates overstep the Cambrian towards the east and south-east, to lie directly on presumed upper Proterozoic siliciclastic sediments in Kronprins Christian Land (Sønderholm & Jepsen 1991; Higgins *et al.* 1991a, b).

Cambrian shelf stratigraphy

The Cambrian of the North Greenland shelf from Peary Land in the east to Nyeboe Land in the west is represented by the Skagen Group (?Early Cambrian), the Portfjeld and Buen Formations (Early Cambrian) and the Brønlund Fjord, Tavsens Iskappe and Ryder Gletscher Groups (Early-Late Cambrian and younger; Fig. 2). Higgins et al. (1991a, b) reviewed these units in terms of the evolution of the Franklinian Basin in Greenland during the Cambrian. Ineson & Peel (1997) proposed formal stratigraphic nomenclature for the Brønlund Fjord and Tavsens Iskappe Groups, and part of the Ryder Gletscher Group (Fig. 2). Ineson & Peel (1997) grouped Cambrian shelf sediments into 3 geographical areas for convenience of description. The main, southern, outcrop belt extends westward from Jørgen Brønlund Fjord in south-east Peary Land, along Wandel Dal, through southern Freuchen Land to southern Warming Land (Figs 1, 2). The type sections of most Lower Cambrian formations lie within this outcrop belt and most of the faunas described herein are also derived from these outcrops. Outcrops from northern Nyeboe Land eastward along the northern coast to the J. P. Koch Fjord area of north-western Peary Land comprise the northern outcrop belt and have yield Lower Cambrian fossils from the Buen and Aftenstjernesø Formations. The eastern outcrop belt includes scattered outcrops in north-east Peary Land around G. B. Schley Fjord; only the Buen Formation has yielded Lower Cambrian fossils in this area (Figs 1-3).

Skagen Group

The Skagen Group (Friderichsen *et al.* 1982) outcrops in isolated exposures from north-east Peary Land to northern Wulff Land. Deposition of the carbonate and siliciclastic strata took place on a storm-dominated shelf following the transgression of the Proterozoic basement. The Skagen Group is the oldest stratigraphic unit of the Franklinian Basin succession in North Greenland; its





Southern Warming Land to southern Freuchen Land

Southern Henson Gletscher region southern Freuchen Land to south-west Peary Land

Løndal region southern Peary Land

base is not exposed. In its type area in north-east Peary Land it is stratigraphically overlain by the Paradisfjeld Group, a deep-water, mainly carbonate unit (Fig. 1). Elsewhere (Peary Land to northern Wulff Land), the Skagen Group is overlain conformably by the Portfjeld Formation, the shelf equivalent of the Paradisfjeld Group (Surlyk & Ineson 1987).

The Skagen Group has not yielded fossils in Greenland but its correlative in Ellesmere Island, the Kennedy Channel Formation, has yielded faunas of Early Cambrian age from its uppermost beds (Dawes & Peel 1984; Long 1989a; Trettin *et al.* 1991).

Portfjeld Formation

The Portfjeld Formation (Jepsen 1971) conformably overlies the Skagen Group in northern outcrops but, to the south, it rests unconformably on Upper Proterozoic strata in its extensive southern outcrop from Wulff Land east to Danmark Ford (Fig. 1). The Portfjeld Formation represents a shallow-water carbonate platform which developed over much of the Franklinian shelf in North Greenland, although no outcrops are known west of Wulff Land. Deeper-water carbonates and siliciclastics equivalent to the Portfjeld Formation in the northern trough succession are assigned to the Paradisfjeld Group (Fig. 1).

The upper surface of the Portfjeld Formation preserves evidence of exposure and karstification, prior to transgression by siliciclastic shelf strata assigned to the overlying Buen Formation. The Portfjeld Formation is 206-290 m thick in southern Peary Land but thins out to the south-east. A representative section from the type area of southern Peary Land is given by Ineson & Peel (1997, fig. 14). The formation thickens markedly towards the north, attaining more than 500 m in north-west Peary Land and northern Freuchen Land area (Higgins *et al.* 1991a).

In southern Peary Land, the formation is dominated by pale grey to yellow weathering, thin-bedded to mediumbedded, cliff-forming dolomites. A persistent unit of dark cherty dolomite forms a distinctive marker in southern Peary Land (Peel 1988b; Ineson & Peel 1997). In northern exposures, the formation is dominated by dolomitised cross-bedded grainstones, with subordinate stromatolitic bioherms. Around the head of Victoria Fjord, a distinctive megabreccia (85-270 m thick) of Portfjeld and other lithologies occurs at this stratigraphic level between the crystalline basement and the Buen Formation.

The Portfjeld Formation has not yielded macrofossils other than stromatolites. Peel (1988b) recorded phosphatised spirally coiled cyanobacteria referred to *Spirellus*, Fig. 2. Lithostratigraphic nomenclature of Cambrian shelf strata in North Greenland (after Ineson & Peel 1997). Lower Cambrian strata are indicated by shading between columns.



Paralleldal region south-east Peary Land

Obruchevella and *Jiangispirellus*, indicating a general late Proterozoic-Early Cambrian age. Dawes & Peel (1984) and Long (1989b) correlated the Portfjeld Formation with the Ella Bay Formation of Ellesmere Island of Early Cambrian age.

Buen Formation

Siliciclastic deposits of the Buen Formation (Jepsen 1971) record the subsidence and subsequent transgression of the eroded carbonate platform represented by the Portfjeld Formation. At its type section on the northern shore of Jørgen Brønlund Fjord (Figs 1, 3) the formation is almost 420 m thick (Ineson & Peel 1997, fig. 15), but it thickens northwards to about 700 m at the transition into the deep-water basin where equivalent strata are referred to the Polkorridoren Group (Higgins *et al.* 1991a; Fig. 1). Within the Buen Formation, a lower sand-dominated member is overlain by an upper mud-dominated member, but the sand content decreases northwards so that the formation is mud-dominated in northern outcrops. Bioturbation and trace fossils are common (Bergström & Peel 1988; Bryant & Pickerill 1990).

The upper mud-dominated strata have yielded abundant macrofossils and two faunas are recognised. At the

North-east Peary Land

Northern Nyeboe Land to north-west Peary Land

base of this mud-dominated unit, trilobites including *Ol*enellus hyperboreus (= *O. (Mesolenellus)* of Palmer & Repina 1993), *Limniphacos perspicullum* and *Serrodis*cus (Table 1) occur together with hyolithids, the bradoriid *Petrianna fulmenta* Siveter, Williams, Peel & Siveter 1996, *Pelagiella* and inarticulate brachiopods (Fig. 3, localities 1, 2, 6). *Olenellus svalbardensis* occurs in the uppermost part of the formation in north-east Peary Land (Fig. 3, localities 3, 4). Examination of acritarch assemblages by Vidal & Peel (1993) confirmed the general late Early Cambrian age of the Buen Formation in its southern outcrop belt.

In northern Freuchen Land, Lane & Rushton (1992) described the problematic Early Cambrian trilobite *Alacephalus? davisi* from the upper part of the formation in association with sponges (Rigby 1986), a bradoriid and undescribed *Olenellus* sp. (J. S. Peel, unpublished observation; Fig. 3, locality 7).

In north-western Peary Land (Fig. 3, locality 5), some few kilometres east of the Freuchen Land locality, an unusual fauna of Burgess Shale type, comprising poorly skeletised arthropods, worms, sponges, articulated halkieriids and other problematic fossils (the Sirius Passet fauna) occurs in mudstones in the lowest part of the formation (Rigby 1986; Budd 1993, 1995; Conway Morris & Peel 1990, 1995; Conway Morris *et al.* 1987; Peel 1990; Peel *et al.* 1992). The presence of the nevadiid tri-



5; Olenellus hyperboreus and Limniphacos perspicultum at localities 1, 2 and 6; Olenellus svalbardensis at localities 3 and 4; Alacephalus? davisi at locality 7. Locality 1, bank of stream immediately south-east of the southern end

of Brillesø, east side of valley of Børglum Elv, southern Peary Land.

Equivalent to Christie & Peel (1977, figure 3, locality 1). GGU collections 100824, 184002, 184007, 184219, 271700, 271798, 271800. Collections are derived from the lower part of the upper mudstone-dominated unit of the Buen Formation, approximately 100 m below the top of the formation (see Vidal & Peel 1993, fig. 2). Locality 2, east of Henson Gletscher, western Peary Land; single collection (GGU 218637) from approximately 60 m below top of Buen Formation. Locality 3, west of G. B. Schley Fjord; a single collection (GGU 256959) 5-10 m below the top of formation. Locality 4, west of G. B. Schley Fjord; a single collection (GGU 256959) 5-10 m below the top of formation. Locality 5, east of J. P. Koch Fjord, western Peary Land; GGU collections 319571, 340103) from mudstones near the base of the formation. This is the locality for the Sirius Passet fauna. Locality 6, west of Sæterdal, two collections (GGU 270590, 270591) approximately 150 m from the top of formation (see Vidal & Peel 1993, figs 1, 2). The collection site lies on the western (left) side of the small creek illustrated by Ineson & Peel (1997, fig. 70). Locality 7, northern Freuchen Land, a few metres below the top of the Buen Formation. GGU collection 319644.

lobite *Buenellus higginsi* indicates an Early Cambrian ("*Nevadella*" Zone) age (Blaker 1988; Conway Morris & Peel 1995; Palmer & Repina 1993). A conspicuous member of the Sirius Passet fauna, *Kleptothule rasmusseni* Budd, 1995, is considered by its author to be a possible olenellinid trilobite (Budd 1995).

Brønlund Fjord Group

Mud-dominated strata of the upper Buen Formation are overlain by carbonates of late Early Cambrian age which introduce the development of the early Palaeozoic carbonate platform that ultimately extended over the entire Franklinian shelf in North Greenland. Cambrian 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 (Figs 1, 2). In the deep-water trough, these strata find equivalence in the Amundsen Land and Vølvedal Groups.

Formation

In southern areas, the Brønlund Fjord, Tavsens Iskappe and Ryder Gletscher Groups record northward progradation of shallow-water carbonate sediments over outer shelf deposits, but this northwards progradation does not explain east-west variation in Cambrian stratigraphy. In western areas of North Greenland, the shelf subsided uniformly through the Cambrian, and a thick succession of mainly platform carbonates accumulated. The eastern margin of the North Greenland craton, however, was uplifted during the Middle and Late Cambrian and the eastern shelf was progressively exposed during the Cambrian. A regional unconformity, developed at the base of





Brønlund Fjord, Tavsens Iskappe and Amundsen Land Groups

30 km

Fig. 4. Localities in the Aftenstjernesø Formation.

Locality 1, north-eastern Nyeboe Land; GGU collection 83337 from the "Aftenstjernesø Formation (?)". This is the source of material described by Peel (1979b: 116) Peel & Larsen (1984) and Dawes & Peel (1984). Locality 2, north-eastern Nyeboe Land; GGU collection 319742. Locality 3, north-eastern Nyeboe Land, south of Kap Bryant; GGU collections 319744-319769; see also Fig. 5. Locality 4, Stephenson Ø; GGU collection 313098 from near the base of the formation.

the succeeding Wandel Valley Formation (upper Lower-Middle Ordovician), decreasing in stratigraphic importance westwards and not recognised farther west than the land area south of Nares Land (Figs 1, 2).

Due to the progressive emergence of the platform in eastern areas during the Cambrian, platform interior facies of Cambrian age assigned to the Ryder Gletscher Group are only locally preserved beneath the Wandel Valley Formation basal unconformity. In more western areas of North Greenland, however, the outer shelf, slope apron and platform margin deposits of the Brønlund Fjord Group and the Tavsens Iskappe Group are conformably succeeded by Cambro-Ordovician platform carbonates assigned to the Ryder Gletscher Group.

Carbonate slope apron and deep, outer shelf sediments of the Brønlund Fjord and Tavsens Iskappe Groups outcropping in the northern outcrop belt from outer J. P. Koch Fjord to northern Nyeboe Land were deposited basinward (northward) of the platform. Sections of the Brønlund Fjord Group in northern Freuchen Land and adjacent north-west Peary Land, within the eastern part of this northern outcrop belt, are readily correlated with the outcrops to the south. West of Nordenskiöld Fjord (Fig. 1), however, the transition from extensive platform carbonates in the south (Ryder Gletscher Group) to the outer shelf facies exposed along the northern coast is buried beneath younger strata. Ineson et al. (1994; see also Ineson & Peel 1997) discussed the stratigraphy of the northern outcrop belt and its importance for an understanding of the evolution of the Cambrian shelf in North Greenland.

The stratigraphy and regional setting of the Brønlund

Fig. 5. Distribution of trilobites within the Aftenstjernesø Formation in northern Nyeboe Land at locality 3 (Fig. 4).

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Fig. 7. Distribution of trilobites within the Kap Troedsson Formation at localities 2 and 4 (Fig. 6).

Kootenia sp. B

Trilobite taxa	BU	AF	KT	HG	S
Peronopsis roddyi				+	
Calodiscus lobatus		+	+		
Ekwipagetia marginata			+		
Pagetides elegans				+	
Pagetides rjonsnitzkii				+	
Serrodiscus daedalus		+			
Serrodiscus latus?		+			
Serrodiscus speciosus		+			
Serrodiscus sp. A.	+				
Buenellus higginsi	+				
Limniphacos perspicullum	+				
Olenellus cf. O. gilberti					+
Olenellus hyperboreus	+				
Olenellus svalbardensis	+				
Olenellus cf. O. truemani			+	+	
Olenellus sp. A			+		
Olenellus sp. B		+			
Ogygopsis batis				+	
Ogygopsis typicalis				+	
Ogygopsis virgata				+	
Olenoides sp. A				+	
Olenoides sp. B				+	
Olenoides sp. C				+	
Bonnia brennus				+	+
Kootenia marcoui				+	+
Kootenia oscari				+	
Kootenia radiata				+	
Kootenia sagena				+	
Kootenia cf. K. 'longa'				+	
Kootenia sp. A				+	
Kootenia sp. B				+	
Kootenia sagena			+		
Dorypygidae gen and sp undet A				+	
Athabaskiella ⁹ sp. A				+	
Zacanthonsis levis				+	
Zacanthonsis contracta				÷	
Zacanthonsis? sn A				÷	
Zacanthoides? sn A				+	
Stephenaspis? avita				+	
Corvnexochid gen and sp undet A				+	
Arthricocephalus chauveaui				+	
Halinlanktos iishouensis				+	
Ovatoryctocara sp. A				+	
Orvetocenhalus vicinus				+	
Lancastria plana				+	
Lancastria? sp. A				÷	
Cheirwoides sp. A				+	
Oryctocenhalid gen and sn undet A		+			
Phychonarella sp. A		•		+	
Ptychoparioid gen and sn undet A				+	
Ptychoparioid gen and sn undet R					+
Ptychoparioid gen and sp undet C					+
Perissonvoe nhenax				+	
Labradoria misera?			+		
Alacenhalus? davisi	+				
Kleptothule rasmusseni	+				
nepronnie rasmasem	1				

Table 1. Stratigraphic distribution of trilobites within the Lower Cambrian of North Greenland.

Fjord Group was described in detail by Ineson & Peel (1997, see also Higgins *et al.* 1991a, b). The Brønlund Fjord Group ranges in age from late Early Cambrian to medial Middle Cambrian. Formations assigned to the group are listed in Fig. 2.

Aftenstjernesø Formation. – The Aftenstjernesø Formation was defined and fully described by Ineson & Peel

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(1997). At its type locality at Henson Gletscher (which is also the type locality of the Henson Gletscher Formation, see Fig. 8A, locality 2) the formation is about 62 m thick (Ineson & Peel 1997, fig. 24), but it varies from 30 m to 130 m within southern Peary Land-Freuchen Land where the formation is dominantly composed of pale, cliffforming dolomites. In northern outcrops the formation is 25-80 m thick and mainly composed of dark, argillaceous limestones and dolomites. A breccia unit occurs at the top of the formation in most sections.

In southern sections it is only the basal phosphoritic carbonates of the formation that are fossiliferous (Member A of the Brønlund Fjord Formation of Christie & Peel 1977 and Frykman 1980). The diverse, but undescribed, fauna includes trilobites (*Bonnia, Calodiscus lobatus,* fragments of *Wanneria*), pelagiellids, inarticulate brachiopods, *Chancelloria, Hyolithellus* and hyolithids (Troelsen 1956; Peel *et al.* 1974; Christie & Peel 1977; Palmer & Peel 1979). Bendix-Almgreen & Peel (1988) described sclerites of *Hadimopanella apicata* which occurs also within the overlying Henson Gletscher Formation and is otherwise reported from the Lower Cambrian of Svalbard (Wrona 1982).

The Aftenstjernesø Formation in north-east Nyeboe Land, south of Kap Bryant (Fig. 4, localities 1-3), is more uniformly fossiliferous when compared to southern outcrops, yielding olenellid trilobites and *Serrodiscus* throughout much of its anomalous 80 m succession (Ineson *et al.* 1994; Fig. 5). This fauna was noted by Peel (1974, 1979), Peel & Larsen (1984), Dawes & Peel (1984) and Higgins *et al.* (1991a). In addition to *Olenellus* sp. B, trilobites include *Serrodiscus speciosus*, *S. daedalus* and *S. latus*? (Table 1). *Latouchella, Chancelloria, Hadimopanella* and hyolithids are also recorded.

Kap Troedsson Formation. – The Kap Troedsson Formation attains a thickness of 25 m at its type section in south-west Wulff Land (Ineson & Peel 1997, fig. 78; locality 2 in Fig. 6) but varies from 10 m to 65 m between Nordenskiöld Fjord and C. H. Ostenfeldt Gletscher (Fig. 1). The formation is a distinctive unit of grey limestones between the underlying recessive shales of the Buen Formation and the overlying brown-weathering cliffs of the dolomitic Bistrup Land Formation. The Kap Troedsson Formation correlates with the thin phosphoritic and glauconitic carbonates forming the basal member of the Aftenstjernesø Formation.

Ineson & Peel (1997) summarised earlier reports of fossils from the Kap Troedsson Formation, in part based on GGU collections 270504 and 270505 examined herein. The trilobite fauna comprises *Calodiscus lobatus, Ekwipagetia marginata, Olenellus* cf. *O. truemani, Olenellus* sp. A, *Labradoria misera*? and *Kootenia* sp. B (Table 1; Fig. 7). Of these, *Olenellus* cf. *O. truemani* also occurs in the Henson Gletscher Formation, while *Calodiscus* was reported from the basal member of the Aftenstjernesø Formation by Christie & Peel (1977).



Fig. 8. Localities within the Henson Gletscher, Sydpasset and Paralleldal Formations.

A, fossiliferous localities within the Henson Gletscher Formation. Locality 1, reference section, southern Freuchen Land (Ineson & Peel 1997, figs 32 and 33): Fig. 10 gives the positions of the fossiliferous samples. Locality 2, type section of the Henson Gletscher Formation (Ineson & Peel 1997, fig. 31; see also Fig. 9). Locality 3, east side of the entrance to Gustav Holm Dal (Fig. 1), western Peary Land; GGU collections 271425 and GGU 271428 from 9 m and 28 m respectively above the base of the formation which is approximately 32 m thick at this locality. Locality 4, south Koch Væg (Fig. 1), western Peary Land. GGU collection 218584 collected at 58 m above the base of the formation (which is 72 m thick in this section) immediately below a sandstone forming the uppermost unit of the formation. Locality 5, section east of J. P. Koch Fjord, western Peary Land (see also Fig. 9). Locality 6, Løndal, east side of Hans Tavsen Iskappe. Reference section (see Fig. 11).

B, fossiliferous localities in the Sæterdal and Paralleldal Formations. Sæterdal Formation: collections from talus blocks (GGU 270563, 270564, 270568, 270579, 270590), and one *in situ* collection (GGU 270584) from approximately 90 m above the base of the formation which is about 130 m thick (cf. Ineson & Peel 1997, fig. 69). The collection locality is illustrated by Ineson & Peel (1997, fig. 70), on the western side (left) of a small stream gully across from the type section. Paralleldal Formation, GGU collection 274908 (Ineson & Peel 1997, fig. 75; lower dark beds of the formation to the left (west) in the photograph).



Fig. 9. Distribution of trilobites within the Henson Gletscher Formation in its type area. Locality 2, the type section west of the snout of Henson Gletscher (2 in Fig. 8A). Locality 5, section north-east of the snout of Henson Gletscher (5 in Fig. 8A).

Henson Gletscher Formation. – The Henson Gletscher Formation was defined and fully described by Ineson & Peel (1997). It is 62 m thick at its type locality at Henson Gletscher (Fig. 8A, locality 2; Fig. 9) but increases to 112 m near Jungersen Gletscher, southern Freuchen Land (Fig. 8A, locality 10). In northern outcrops it varies between 20 m and 90 m. Dark weathering, recessive, sooty limestones, mudstones and dolomites contrast with a central unit of pale weathering sandstones in most sections, but the sandstones are less conspicuous in northern sections. In Løndal (Fig. 8A, locality 6), coarse skeletal packstones and grainstones occur near the base of the formation.

The Henson Gletscher Formation has yielded faunas of late Early Cambrian to late Middle Cambrian age (Palmer & Peel 1979; Blaker 1986; Blaker *et al.* 1997; Peel & Blaker 1988; Peel 1989, 1994a; Ineson & Peel 1997). The relative distribution of these faunas within the formation varies strongly throughout the region and the top of the formation is strongly diachronous (Ineson & Peel 1997). The type section and adjacent sections (Fig. 8A, localities 2, 3, 5; Fig. 9) yielded no olenellids and the assignment of trilobites to the Early Cambrian is based on faunal comparisons with sections in southern Freuchen Land and Løndal (Fig. 8A, localities 1, 6; Figs 10, 11). The upper beds in the type section (Fig. 9, 55-62 m), however, are richly fossiliferous (Middle Cambrian, *Ptychagnostus gibbus* Zone), but early Middle Cambrian faunas have not been located.

Palmer & Peel (1979) suggested the presence of a discontinuity within the Henson Gletscher Formation as an explanation for the absence of lower Middle Cambrian strata, but no discontinuity has been recognised on lithological grounds in the condensed succession. Ineson & Peel (1980) equated the inferred unconformity with the Hawke Bay Event which was recognised by Palmer & James (1980) as being a circum-Iapetus tectonic event. Interestingly, at least some of the supposedly "missing" time interval is represented in North-West Greenland, from where early Middle Cambrian faunas have been documented by Poulsen (1927, 1964). In addition, early Middle Cambrian faunas occur in the Henson Gletscher Formation at Hand Bugt in northern Nyeboe Land (Peel 1994a; Figs 1, 4).

The reference section of the Henson Gletscher Formation in southern Freuchen Land (Fig. 10) yields rich faunas of Early Cambrian age, including olenellids, but no Middle Cambrian faunas. The section in Løndal (Fig. 11) yields medial Middle Cambrian agnostoids only from its uppermost beds but a rich Early Cambrian fauna.



Fig. 10. Distribution of trilobites within the Henson Gletscher Formation at locality 1 in southern Freuchen Land (Fig. 8A).

Sections in northern Nyeboe Land described by Ineson *et al.* (1994) have not yielded Early Cambrian faunas but extensive early Middle Cambrian (*Glossopleura* Zone) and younger faunas are reported (Babcock 1994a, b; Peel 1994b; Robison 1994).

Thirty five of the 55 species of Lower Cambrian trilobites described herein were collected from the Henson Gletscher Formation but only 3 of these species occur in other formations in North Greenland (Table 1). There is little doubt that the abundance and fine state of preservation of the fossils of the Henson Gletscher Formation have focused the present study on its trilobite faunas. Blaker (1986) presented a preliminary assessment of the Early Cambrian trilobites of the Henson Gletscher Formation, based on the section in southern Freuchen Land (Fig. 8A, locality 1). Substantial revision of these preliminary identifications is undertaken herein.

Sæterdal Formation. – In general, the pale sandstones of the Sæterdal Formation (Ineson & Peel 1997) are poorly fossiliferous although locally beds yield faunas of trilobites and brachiopods (*Kutorgina* and *Nisusia*). The formation attains a thickness of 130 m at its type locality in Sæterdal (just north-east of the fossil locality in Fig. 8B) but thins to the east and west. It conformably overlies the Aftenstjernesø Formation and intergrades laterally with the Henson Gletscher Formation (Fig. 2). Preliminary fossil determinations were given by Palmer & Peel (1979).



Fig. 11. Distribution of Lower Cambrian trilobites within the Henson Gletscher Formation in Løndal (locality 6 in Fig. 8A).

Kootenia marcoui and Bonnia brennus are conspicuous, also occurring in the Henson Gletscher Formation; they are associated with Olenellus cf. O. gilberti and undetermined pychoparioid trilobites (Table 1). Paralleldal Formation. – Cliff-forming pale dolomites of this formation attain a maximum thickness of 165 m on the north side of Paralleldal (Fig. 8B), but the formation thins to the west and east (Ineson & Peel 1997). In west-

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ern outcrops the formation conformably overlies the Sæterdal Formation but to the east the formation lies conformably directly on the Aftenstjernesø Formation (Fig. 2). Throughout its outcrop, the Paralleldal Formation is unconformably overlain by upper Lower Ordovician dolomites of the Wandel Valley Formation.

Undescribed silicified fragments of olenelloid and other trilobites occur together with *Kutorgina* and other brachiopods, *Yochelcionella, Cambridium* and *Latouchella* in dark bioturbated dolomites forming the lower part of the formation at Paralleldal, north of Jørgen Brønlund Fjord, southern Peary Land (GGU collection 274908; Fig. 8B). Archaeocyathans described by Debrenne & Peel (1986) and *Salterella maccullochi* described by Peel & Yochelson (1982) indicate a middle-late Toyonian (latest Early Cambrian; latest *Olenellus* Zone) age.

Biostratigraphy and correlation

Neither the lower nor the upper boundary of the Lower Cambrian is well constrained in North Greenland in terms of fossil faunas. Dimensions of the spiral cyanobacteria described by Peel (1988b) from the Portfjeld Formation suggest an age near the Precambrian-Cambrian boundary, but sparse faunas from the uppermost Kennedy Channel Formation in adjacent Arctic Canada (Long 1989a), apparently equivalent to the upper part of the unfossiliferous Skagen Group of North Greenland, include fragments of trilobites. Thus, the base of the Cambrian must lie low in the Skagen Group or in some stratigraphically lower, unexposed unit.

In sections of the southern outcrop belt (Fig. 2), Early Cambrian faunas are followed by medial Middle Cambrian faunas (Ptychagnostus gibbus Zone) in condensed successions within the Henson Gletscher Formation without lithological evidence of disconformity (Fig. 9). Poulsen (1964) has suggested that in inner shelf successions in Inglefield Land, North-West Greenland (Fig. 1), the Plagiura-Poliella Zone (equivalent to the latest Toyonian) is represented by clasts within later sediments assigned to the Glossopleura Zone (Cape Wood Formation) which overlie limestones of the Cape Kent Formation with Bristolia; the intervening Albertella Zone (Middle Cambrian) is not documented. Henson Gletscher Formation with Glossopleura is reported from northern Nyeboe Land (Babcock 1994a; Fig. 12, fauna 8) and this zone is also recognised in North-West Greenland (Poulsen 1927, 1964). The precise relationship, however, between these faunas and older, Early Cambrian, faunas is uncertain.

Fritz (1972) recognised 3 trilobite zones within the Lower Cambrian of Laurentia: *Fallotaspis, Nevadella* and *Bonnia-Olenellus* Zones in ascending order. After discuss-

F	SIBERIAN PLATFORM	CHINA	LAUF archaeocyaths	RENTIA trilobites	NORTH GREENLAND	
Low	er Amgan			Glossopleura	8	
	Oryctocara			Albertella	1	
an	A. splendens			Plagiura/Poliella	Henson	*********
yoni	Lermontovia grandis	Megapalaeolenus	T. greenlandicus P. pearylandicus		5 Gletscher	7 Paralleldal
۲Ĕ	B. ketemensis			Olenellus		6 Sæterdal
	B. ornata			Olenellus	٨٩٠٣	0 Octordar
nia	B. asiaticus				4 Altens	gemesø
pton	B. gurarii				3	
ă	B. micmacciformis - Erbiella				2 Ві 1	Jen
ш	F. lermontovae			"Nevadella"	Por	tfjeld
ani	N. kokoulini				Skager	Group
dab	C. pinus			"Fallotaspis"	Okagei	loloup
At	R. zegebarti	19 19			1	
٦	Tommotian					

Fig. 12. Correlation of North Greenland formations compared to the Early Cambrian (Tommotian – Toyonian) and earliest Middle Cambrian (Amgan) of Siberia and Laurentia. 1-7 indicate Lower Cambrian faunas discussed in the text; 8 is the *Glossopleura* assemblage described by Babcock (1994a).

ing the content and various uncertainties surrounding the use of these zones, Palmer & Repina (1993) proposed that the 3 zones be termed "Fallotaspis" Zone, "Nevadella" Zone and Olenellus Zone; this suggestion is followed here.

Biostratigraphy

Lower Cambrian faunas of North Greenland range in age from the upper "Nevadella" Zone through the overlying Olenellus Zone in terms of the Laurentian standard (cf. Palmer & Repina 1993; Fig. 12). In Siberian terms, this range is encompassed within the latest Atdabanian (or possibly early Botomian), through the Botomian and the Toyonian (Zhuravlev 1995, table 1). The boundary with the overlying Middle Cambrian is poorly known in North Greenland, on account of a lack of fossil collections but, as noted above, several sections through the Henson Gletscher Formation cross the boundary.

The oldest age diagnostic Cambrian fauna in North Greenland, and probably within Greenland as a whole, is recorded from the lower Buen Formation where *Buenellus higginsi* occurs with other members of the Sirius Passet Fauna, including *Kleptothule rasmusseni*, at the northernmost margin of the carbonate platform represented by the Portfjeld Formation (Fig. 3, locality 5; Fig. 12, fauna 1). Palmer & Repina (1993) considered *Buenellus* to be indicative of the "*Nevadella*" Zone of the Laurentian standard. This can be equated with the late Atdabanian or early Botomian of Siberian usage (Zhuravlev 1995).

In the upper part of the Buen Formation in southern Peary Land (Fig. 3, locality 1; Fig. 12, fauna 2), the occurrence of Olenellus hyperboreus (type species of Olenellus (Mesolenellus) Palmer & Repina 1993) together with the nevadiid Limniphacos perspicullum gen. et sp. nov. suggests an age close to the boundary between the "Nevadella" Zone and the Olenellus Zone, possibly lowermost Olenellus Zone. Exposures a few metres higher yield only O. hyperboreus. Palmer & Repina (1993:11; see also Fritz 1992) commented on the abrupt faunal boundary between the "Nevadella" Zone and the overlying Olenellus Zone in Laurentia. Unfortunately, Limniphacos is currently known only from Greenland.

Uppermost beds of the Buen Formation yield Olenellus svalbardensis (Fig. 3, localities 3 and 4) and Alacephalus? davisi (locality 7). Other species of Olenellus occur within the overlying Aftenstjernesø, Kap Troedsson, Henson Gletscher and Sæterdal Formations, indicating the Olenellus Zone (Fig. 12, fauna 3).

The Kap Troedsson Formation and the equivalent basal beds of the Aftenstjernesø Formation together contain a fauna including *Calodiscus lobatus*, *Ekwipagetia marginata*, *Olenellus* cf. *O. truemani*, *Serrodiscus speciosus* and other species of *Serrodiscus*; tiny fragments of exoskeleton with characteristic *Wanneria* ornament are also present suggesting a medial *Olenellus* Zone age (Table 1, Fig. 12, fauna 4). The occurrence of the geographically widely distributed *Calodiscus lobatus* is noteworthy but of uncertain stratigraphic significance (see Ahlberg & Bergström 1993 and discussion below).

The overlying Henson Gletscher Formation is diachronous throughout the region (and individual sections may be entirely of Middle Cambrian age (northern Nyeboe Land; Figs 2, 4, 12; see Peel 1994a), of Early-Middle Cambrian age (Figs 8A, 9, localities 2, 5 and 6) or entirely of Early Cambrian age (Fig. 8A, locality 1; Fig. 10).

Within the Henson Gletscher Formation, Olenellus cf. Olenellus truemani occurs throughout the succession in southern Freuchen Land (Fig. 8A, locality 1; Fig. 10). In the lowest beds it is associated with Ogygopsis batis and Cheiruroides sp. A, but Arthricocephalus chauveaui, Oryctocephalus and other oryctocephalids, Ogygopsis spp., Kootenia spp., Zacanthopsis levis, Peronopsis roddyi and Stephanaspis? avita soon appear, while Bonnia brennus and Pagetides elegans join the olenellid in the highest fossiliferous collections (Fig. 10). This fauna (Fig. 12, fauna 5) seems to be a middle to late Toyonian assemblage, equivalent to the highest Olenellus Zone. It is thus equivalent in age to the Paralleldal Formation in its type area which yields archaeocyathans of middle to late Toyonian age (Debrenne & Peel 1986; Fig. 8B; Fig. 12, fauna 7). Elsewhere in the Paralleldal Formation, Salterella maccullochi indicates a late Olenellus Zone (Peel & Yochelson 1982). The Sæterdal Formation yields Olenellus cf. O. gilberti, Bonnia brennus, Olenoides sp. C and ptychoparioids (Table 1, Fig. 12, fauna 6), of which B. brennus occurs in the highest fossiliferous beds of the Henson Gletscher Formation in southern Freuchen Land and Løndal (Figs 10, 11).

In the Henson Gletscher Formation in Løndal (Fig. 8A, locality 6; Fig. 11), Oryctocephalus vicinus, P. elegans and B. brennus occur above the highest occurrence of olenellids, but they are assumed to be of Olenellus Zone age. In the area of the type section (localities 2, 3, 5; Figs 8A, 9), olenellids and B. brennus have not been collected and the age of the stratigraphically highest collections referred to the Early Cambrian in the poorly fossiliferous sections is determined on the basis of the occurrence of O. vicinus, P. elegans and Lancastria plana which occur together with olenellids at other localities in the Henson Gletscher Formation. It should be noted, however, that C. vicinus and L. plana were originally described from Russian outcrops considered to be of earliest Middle Cambrian age by Chernysheva (1962) and Tomashpolskaya & Karpinskii (1962).

In general terms, the two principal sections through the Henson Gletscher Formation (southern Freuchen Land, locality 1; Løndal, locality 6 in Figs 8A, 10, 11) show a faunal succession from *Kootenia* spp. and *Ogygopsis* spp. to oryctocephalids, *Bonnia brennus* and *Pagetides elegans*. This sequence of faunas is associated with increasingly outer shelf conditions, but the extent to which the

sequence of faunas is controlled by changing environments or is time-dependent (*i.e.*, of biostratigraphic utility) is unresolved.

Correlation

Recent studies of Middle Cambrian trilobite faunas from North Greenland have demonstrated the value of this area in terms of international correlation within the Cambrian and increased understanding of Cambrian palaeogeography (Robison 1988, 1994; Hood & Robison 1988; Babcock 1994a, b). Structurally uncomplicated Cambrian sections through platform to deep-water trough successions (cf. Ineson & Peel 1997) offer clear insight into the relationship between shallow, warm-water, nearshore trilobite faunas and deeper, cool-water, offshore faunas around the Laurentian continent.

A notable example is provided by latest Middle Cambrian faunas collected along a north-south transect from platform to outer shelf in the Franklinian Basin succession along J. P. Koch Fjord (Fig. 1). Robison (1988) described a rich inner shelf fauna from the Holm Dal Formation in Gustav Holm Dal, just east of the head of J. P. Koch Fjord (Fig. 8A, adjacent to locality 3). Forty two out of the 43 described polymeroid species (indicative of the lower-middle Cedaria Zone as widely applied in North America) occur only within Laurentia, whereas at least 13 out of 15 agnostoid species (Lejopyge laevigata Zone) had intercontinental distributions in open-shelf and basinal facies. Some 40 km to the north (south of locality 5 in Fig. 3), down slope towards the basin, Robison (1994) and Babcock (1994a, b) described faunas of the same age of Baltic aspect. These equatorial (in the Cambrian) deep water, outer-shelf faunas are taxonomically most similar to high latitude, cool-water faunas best known from around Baltica which were located at about 60 degrees south in the Cambrian. Faunas of mixed composition characterise strata of the same age in northern Nyeboe Land which occupy an intermediate position in terms of environment. Babcock (1994a, b) attributed this segregation of faunas, the classic Atlantic (=Baltic) and Pacific (=Laurentian) faunas of previous authors, to the presence of a thermocline around the Laurentian continent in the Middle Cambrian. As a consequence of this co-occurrence of faunas of Laurentian and Baltic aspect, Robison (1988, 1994) was able to verify earlier suggestions that the Cedaria Zone, the basal zone of the Dresbachian and traditionally the earliest zone of the Late Cambrian in North America, was largely equivalent to the uppermost Middle Cambrian Lejopyge laevigata Zone of the Swedish standard succession.

North Greenland preserves one of the most diverse trilobite faunas known from the late Early Cambrian, with the majority of the 55 species coming from the Henson Gletscher Formation. These Lower Cambrian faunas also offer possibilities for correlation between Laurentia and other Cambrian continents, principally on account of the presence of outer shelf species. Noteworthy are occurrences of oryctocephalids enabling correlation from China through Siberia to North Greenland to Avalonia (Newfoundland), and ultimately into Laurentia.

Svalbard. – In Svalbard, Major & Winsnes (1955), Kielan (1960) and Birkenmajer & Orlowski (1977) described Lower Cambrian faunas from the Hekla Hoek succession at Hornsund and Sørkapp. Cowie (1974: 127-128) described the faunas as "... a Pacific Province fauna [on account of the *Olenellus* spp.] with some affinities with the Atlantic Province shown by the presence of species of *Serrodiscus* and *Calodiscus*". The faunas, however, are of similar aspect to that from Laurentian North Greenland, particularly the Aftenstjernesø Formation of northern Nyeboe Land and the upper Buen Formation.

Species level correlation exists with regard to Olenellus svalbardensis, described by Kielan (1960), Orlowski in Birkenmajer & Orlowski (1977) from Hornsund and by Poulsen (1974) from easternmost North Greenland. In Svalbard this species occurs in the Blåstertoppen Dolomite Formation and in overlying black shales of the Vardepiggen Formation while the Greenland occurence is from the uppermost Buen Formation. Kielan (1960) also identified a poorly preserved Nevadia from loose material considered to be derived from the shales, but this was considered to be an indeterminate olenellid by Cowie (1974) and Birkenmajer & Orlowski (1977). The occurrence of Olenellus svalbardensis in the underlying Blastertoppen Dolomite Formation confirms the miss-identification as a nevadiid. Wrona (1982) described the paleoscolecidan sclerite Hadimopanella apicata from the Blåstertoppen Dolomite Formation. In North Greenland, H. apicata occurs within the Aftenstjernesø and lower Henson Gletscher Formations (Bendix-Almgreen & Peel 1988).

Major & Winsnes (1955) described *Olenellus*, *Calodiscus* and *Serrodiscus* from the Slaklidalen Limestone Formation, a similar association is known the Aftenstjernesø Formation in northern Nyeboe Land (Fig. 5).

The tripartite division of dark shales between two carbonate formations in the Hornsund area invites lithological correlation with the Portfjeld and Buen Formations and the overlying Brønlund Fjord Group of North Greenland. Such correlation is unlikely; the lower Buen Formation and the underlying Portfield Formation are of "Nevadella" Zone age, while the olenelloids from the Blastertoppen Dolomite Formation of Hornsund indicate the Olenellus Zone. Lithological correlation between the 2 areas is therefore unsure, unless all the Hornsund succession is equivalent to the Aftenstjernesø Formation. Interestingly, the Blåstertoppen Dolomite Formation overlies argillaceous strata which might be lithologically similar to the Buen Formation, the Gåshamna Phyllite Formation, but Birkenmajer & Orlwoski (1977) considered this unit to be of Precambrian age.

Greenland. – Rich faunas of Lower Cambrian trilobites were described from platform strata now assigned to the Ryder Gletscher Group from Inglefield Land, North-West Greenland, by Poulsen (1927, 1958a, 1964; see also Poulsen 1946; Figs 1, 2). Almost all taxa were described as new species. In addition to olenellids referred to *Bristolia, Wanneria, Olenellus* and *Paedeumias*, there are species of *Dolichometopsis, Inglefieldia, Kochiella* and *Poulsenia*. None of these platform species is recognised within faunas described herein from the platform margin and slope facies of the Brønlund Fjord Group. The occurrence of *Bristolia* in the Cape Kent Formation may suggest a latest *Olenellus* Zone age, equivalent to the Middle Toyonian faunas of the Henson Gletscher Formation.

One Middle Cambrian generic name, *Ptychoparella* Poulsen, 1927, is applied to a variable species from the Henson Gletscher Formation. The Inglefield Land faunas are of late Early Cambrian age (*Olenellus* Zone) and occur in carbonates overlying the Dallas Bugt Formation (Peel *et al.* 1982) which is a more inshore, directly correlative equivalent of the upper Buen Formation.

Lower Cambrian faunas from North-East Greenland were described by Poulsen (1932), but detailed faunal lists were given by Cowie & Adams (1957). Most taxa described by Poulsen (1932) were proposed as new species but Cowie (1971) lists Calodiscus lobatus and Olenellus cf. O. truemani from limestones within the mainly siliciclastic sediments of the upper Bastion Formation, both of these species are described herein from the Kap Troedsson Formation (Table 1). A diverse fauna also occurs within the limestones of the overlying Ella Island Formation and the fauna as a whole is clearly Olenellus Zone. The highest known Lower Cambrian fossils are specimens of Salterella maccullochi from dolomites of the Hyolithus Creek Formation; these occurrences, and records of the same species in the Paralleldal Formation of North Greenland, are described by Peel & Yochelson (1982).

North America. – The numerous polymerid trilobites from the Cambrian of North Greenland have their closest affinities with faunas from elsewhere in North America, as would be expected from the Cambrian continental reconstruction of Scotese & McKerrow (1990) and the well-known endemism of these forms (cf. Robison 1988; Babcock 1994a, b).

The Saline Valley Formation of western Nevada has yielded a fauna of strikingly similar composition to that of the Henson Gletscher Formation (Palmer 1964; Figs 10, 11; Fig. 12, fauna 5). Ogygopsis batis, Stephenaspis? avita, Kootenia oscari and Zacanthopsis contracta are common to both faunas, associated with Lancastria (=Goldfieldia of Palmer 1964), olenellids, Bonnia and Ptychoparella (=Syspacephalus of Palmer 1964). Accompanying olenellids are unlike the Henson Gletscher forms and may suggest a slightly older age. Higher beds in the same area contain Bristolia and may be equivalent to the inner shelf Cape Kent Formation of Inglefield

Land, North-West Greenland. *Bristolia* is not recognised in the outer shelf Henson Gletscher Formation. Several of these species also occur in the Pioche Shale in Nevada (Fritz 1968). Of these, *Z. levis* also occurs in Virginia and Quebec, while *O. batis* is further recognised from the Lower Cambrian of Siberia (Chernysheva 1971; Egorova *et al.* 1976; Rozanov *et al.* 1992). *Bonnia brennus* described herein from the Henson Gletscher Formation was originally described from the Lower Cambrian of Quebec (cf. Rasetti 1948).

The agnostid *Peronopsis roddyi* and the eodiscoids *Calodiscus lobatus, Ekwipagetia marginata, Pagetides elegans, Serrodiscus speciosus* and *S. latus*? offer correlation with Newfoundland, Quebec and the Taconic sequence in eastern North America (Rasetti 1967). With the Lower Cambrian Sekwi Formation of the Yukon, the North Greenland faunas share *Olenellus* cf. *O. gilberti* and *Perissopyge phenax*.

Ogygopsis virgata is recognised from Alaska (Hillard Limestone, as *O. antiqua* Palmer, 1968), Nevada (Harkless Formation) and Siberia (Chernysheva 1971). *O. typicalis*, reported here from the Henson Gletscher Formation, is previously described from the Middle Cambrian Naomi Peak Limestone of Utah and Idaho.

Intercontinental correlations. - Palmer (1972) noted that the shelf-margin regions of Siberia include many elements found in faunas from similar regions of western Laurentia. Thus, it is not unexpected that shelf deposits from North Greenland, such as the Henson Gletscher Formation, also contain forms distributed in similar facies around other Cambrian continents. Alacephalus Repina 1960 from the Altai Sayan fold belt of Siberia was tentatively identified within the upper Buen Formation of Freuchen Land by Lane & Rushton (1992). Palmer & Repina (1993: 31) recorded Buenellus from Novaya Zemlya, but this Russian record is unsupported (A. R. Palmer, personal communication 1996). Other North Greenland taxa with Siberian distributions include Ogygopsis batis (Chernysheva 1971, as O. siberica; Egorova et al. 1976; Rozanov et al. 1992) from the late Toyonian and O. virgata (Chernysheva 1971), as noted above.

Eodiscoid trilobites are considered to be among the best index fossils for regional and global correlation of upper Lower Cambrian strata (Ahlberg 1984). Calodiscus lobatus, a species that is geographically widespread in the North Atlantic region, including North and North-East Greenland (see above and Ahlberg & Bergström 1993), is also recognised in Kazakhastan. In North Greenland C. lobatus appears to have a very restricted vertical distribution, being confined to the lowest carbonates of the Kap Troedsson Formation (Fig. 7) and Aftenstjernesø Formation which overlie the siliciclastic sediments of the Buen Formation. It is also reported by Cowie (1971) from the Upper Bastion Formation of North-East Greenland and all these Greenland occurrences seem to correlate with the Scandinavian records (Holmia kjerulfi Zone) noted by Ahlberg & Bergström 1993).

However, Landing (1992, see also Zhuravlev 1995) noted the long range of this species in eastern New York, stressing that the more restricted stratigraphic occurrences in other continents do not permit great precision in correlation.

Calodiscus lobatus occurs together with Ekwipagetia marginata and Serrodiscus speciosus in the Elliptocephala fauna of the Taconic sequence of north-eastern North America (Rasetti 1967). S. speciosus has a wide geographical distribution from Laurentia, Siberia (as its junior synonym Serrodiscus levis) and several European countries.

Serrodiscus daedalus was first described from the Cymbric Vale Formation, New South Wales, Australia (Öpik 1975) and is also recognised here from Siberia (Okuneva & Repina 1973) and the Aftenstjernesø Formation of North Greenland. S. latus?, originally described by Rasetti (1966b) from the Taconic sequence of New York is also reported from the Aftenstjernesø Formation. Zhuralev (1995) noted that the distribution of the Serrodiscus-Calodiscus assemblage on the Siberian platform was of Botomian age and not latest Atdabanian, as suggested by Robison et al. (1977) and others. Greenland occurrences arc well up in the Olenellus Zone.

Pagetides rjonsnitzkii, identified here from the Henson Gletscher Formation, was originally described from eastern Siberia by Lermontova (1940).

Oryctocephalids appear to be of considerable value for correlation (cf. Figs 9-11). Particularly noteworthy is the recognition of Arthricocephalus chauveaui from the Henson Gletscher Formation of North Greenland; the genus was previously known only from localities in China (e.g. Zhang 1980a, b; Zhou & Yuan 1981) where it occurs in the upper part of the Tsanglangpu (Canglangpu) Stage (Megapalaeolenus Zone; Fig. 12). A. chauveaui also occurs in Siberia, as Oryctocarella Tomashpolskaya & Karpinskii, 1962 and Oryctocara (Ovatoryctocara) granulata Chernysheva, 1962 (but not material subsequently assigned to this species by Egorova et al. 1976 and Savitsky et al. 1972). Oryctocara granulata is also reported from the upper Brigus Formation of Branch Cove, Newfoundland (Robison et al. 1977; Bengtson & Fletcher 1983; Landing 1992; Zhuravlev 1995) but no published description of the material is available. In the recent compilation by Zhuravlev (1995, Table 1), the Megapalaeolenus Zone of China is considered to be Middle Toyonian age, directly correlative with the archaeocyathid assemblage described from North Greenland by Debrenne & Peel (1986). Occurrences of A. chauveaui in the Henson Gletscher Formation are of closely similar age (Fig. 12).

Haliplanktos jishouensis is described from the Henson Gletscher Formation and the Lower Cambrian of southern China (Zhou et al. 1977). Ovatoryctocara sp. A from the Henson Gletscher Formation is also recognised in Siberia, as O. (Ov.) granulata Chernysheva, 1962 sensu Savitsky et al. 1972 and Egorova et al. 1976 (non Chernysheva 1962). Lancastria plana was originally described from the earliest Middle Cambrian of the Altai Sayan (cf. Tomashpolskaya & Karpinskii 1961), but occurs in the late Early Cambrian Henson Gletscher Formation. In China, the genus is recognised as *Changaspis* and *Chienaspis* which also occur in the *Megapalaeolenus* Zone (Fig. 12).

Thus, following Zhuravlev (1995, table 1; Fig. 12), correlation is possible from the *Megapalaeolenus* Zone of China, through the middle Toyonian *Lermontovia grandis* Zone of Siberia, to the archaeocyath *Tergerocyathus greenlandicus/Pycnoidocyathus pearylandicus* Zone of North Greenland (Laurentia). This is confirmed by the correlation between the *Megapalaeolenus* Zone and the Henson Gletscher Formation based on oryctocephalids described herein. From the Henson Gletscher Formation might be extended into North America (Saline Valley Formation?) and possibly eastern Newfoundland (*Oryctocara granulata*), although Zhuravlev (1995) suggested a correlation of the latter with the lowest Middle Cambrian.

Oryctocara granulata (part), Oryctocephalus vicinus and Lancastria plana were originally described from early Middle Cambrian occurrences in Siberia and are now described from the latest Early Cambrian Henson Gletscher Formation of Greenland where they occur together with olenellids. If these identifications can be maintained, they highlight the current uncertainty concerning the placement of the boundary between the Early and Middle Cambrian (Geyer & Landing 1995; Geyer & Palmer 1995). Assuming the first appearance of Paradoxides sensu lato to be indicative of the base of the Middle Cambrian, it has been suggested that much of the Olenellus Zone (and all the Toyonian of the Siberian standard) might come to be classified as Middle Cambrian (Geyer & Palmer 1995, fig. 1; Debrenne & Debrenne 1995, table 4). As pointed out by Geyer & Palmer (1995), this action is premature and in the present context, the Toyonian is retained within the Early Cambrian (Fig. 12).

Systematic Descriptions

Material used in this study is identified by either specimen or collection numbers in combination with depository abbreviations. GGU, Grønlands Geologiske Undersøgelse (Geological Survey of Greenland, now part of the Geological Survey of Denmark and Greenland), Copenhagen, Denmark. MMH and MGUH, Geological Museum, Copenhagen, Denmark. The location of other type or figured material is given in the text. A key to cited GGU collection numbers is given in Table 2.

Order Agnostida Salter 1864

Diagnosis. – Following Robison (1984: 9), agnostids have basal lobes on cephalon, no articulating half ring on anterior thoracic segment, and no overlap between

GGU	Formation	Figs	Loc.	GGU	Formation	Figs	Loc.
83337	Aftenstjernesø	4	1	298547	Henson Gletscher	8A, 10	1
100824	Buen	3	1	298553	Henson Gletscher	8A, 10	1
184002	Buen	3	1	298979	Kap Troedsson	6.7	2
184007	Buen	3	1	298982	Kap Troedsson	6.7	2
184219	Buen	3	1	298983	Kap Troedsson	6,7	2
218584	Henson Gletscher	8A	4	298984	Kap Troedsson	6	3
218608	Henson Gletscher	8A.9	5	301336	Henson Gletscher	8A 10	1
218610	Henson Gletscher	8A. 9	5	301338	Henson Gletscher	8A 10	1
218611	Henson Gletscher	8A. 11	6	301340	Henson Gletscher	8A, 10	1
218637	Buen	3	2	301341	Henson Gletscher	8A, 10	1
225702	Henson Gletscher	8A. 11	6	301342	Henson Gletscher	8A. 10	1
225703	Henson Gletscher	8A. 11	6	301343	Henson Gletscher	8A, 10	1
225704	Henson Gletscher	8A. 11	6	301344	Henson Gletscher	8A, 10	1
225706	Henson Gletscher	8A 11	6	301346	Henson Gletscher	8A 10	i
225707	Henson Gletscher	8A. 11	6	301349	Henson Gletscher	8A, 10	î
225709	Henson Gletscher	8A 11	6	301351	Henson Gletscher	8A 10	1
225712	Henson Gletscher	8A 11	6	313098	Aftenstiernesø	4	7
225714	Henson Gletscher	8A 11	6	310769	Aftenstiernesø	4 5	3
256959	Buen	3	3	315049	Kan Troedsson	67	4
270504	Kan Troedsson	6	i	315051	Kan Troedsson	6.7	4
270505	Kap Troedsson	6	1	315087	Henson Gletscher	84 10	1
270563	Sæterdal	88		315088	Henson Gletscher	84 10	i
270564	Sectordal	8B		315000	Henson Gletscher	84 10	1
270568	Sæterdal	8B		315003	Henson Gletscher	84 10	1
270570	Sectordal	8B		315095	Henson Gletscher	8A 10	1
270584	Sæterdal	80		315006	Henson Gletscher	8A 10	1
270500	Sectordal	8B		315007	Henson Gletscher	84 10	1
270501	Ruon	3	6	315000	Hanson Glatscher	8A 10	1
270502	Buen	3	6	315107	Henson Gletscher	8A 10	1
270392	Buen	3	4	3151107	Henson Glatscher	8A, 10	i
271425	Hanson Glatschar	<u>Э</u> 8 л	2	215110	Henson Glatscher	8A 10	1
271423	Henson Gletscher	0	2	315140	Kan Troedsson	6 7	2
271420	Henson Cletscher	0 9 A O	2	215145	Kap Troadeson	67	2
271403	Henson Clatashan	04,9	2	215174	Kap Treedeen	6, 7	2
271403	Henson Cletscher	0A, 9	2	313174	Rup Hoeusson	2	2
271400	Dues Dietscher	0A, 9	2	210571	Duen	2	5
271745	Buen Hansan Clatashan	3 9 A 11	6	319371	Afternationnand	3	2
271743	Henson Gletscher	0A, 11	6	319742	Aftenstjernesø	4	2
2/1/48	Henson Gletscher	8A, 11	0	319744	Antenstjernesø	4, 5	2
271750	Henson Gletscher	8A, 11	0	319755	Aftenstjernesø	4, 5	3
271752	Henson Gletscher	8A, 11	0	319757	Aftenstjernesø	4, 5	3
2/1/55	Henson Gletscher	8A, 11	0	319759	Aftenstjernesø	4, 5	3
2/1/30	Henson Gletscher	8A, 11	6	319760	Aftenstjernesø	4, 5	3
2/1/98	Buen	3	1	319761	Attenstjernesø	4, 5	3
271800	Buen	3	1	319762	Aftenstjernesø	4, 5	3
2/1908	Paralleldal	8B		319763	Attenstjernesø	4, 5	3
298537	Henson Gletscher	8A, 10	1	319/64	Attenstjernesø	4, 5	3
298539	Henson Gletscher	8A, 10	1	319765	Attenstjernesø	4, 5	3
298544	Henson Gletscher	8A, 10	1	319769	Attenstjernesø	4, 5	3
298545	Henson Gletscher	8A, 10	1	340103	Buen	5	5

Table 2. Key to GGU collections cited in the text. Collections are derived from numbered localities identified within the indicated figure.

cephalon and thorax. The labrum has unusually long anterior and posterior wings, and the thorax has two segments.

Remarks. – A review of trilobite classifications is given by Moore (1959). Robison (1987, 1988) and others have classified the trilobites into two orders, Agnostida (including eodiscoids) and Polymerida. Recent studies by Müller & Walossek (1987, see also Walossek & Müller 1990) have questioned the assignment of agnostids to the trilobites but Fortey & Theron (1995) considered it unwise to exclude agnostids from the trilobites at the present time. In the present context, where biostratigraphy rather than phylogeny is the main focus, agnostids are regarded as a trilobite order for convenience. Eodiscids are separated from agnostids but are not assigned at ordinal level (see Babcock 1994a) while other polymerid trilobites are divided into several orders.

Agnostids are amongst the best index fossils for global correlation of the Middle and Upper Cambrian (cf. Robison 1984, 1988, 1994). They are rare in Lower Cambrian strata, previously only being known from eastern North America (Resser & Howell 1938; Rasetti & Theokritoff 1967) and Warwickshire, England (Rushton 1966). The discovery of Lower Cambrian agnostids from the Henson Gletscher Formation of Freuchen Land and Peary Land is therefore noteworthy, particularly as direct correlation is established with the Taconic Sequence of Washington County, New York State, U. S. A.

Family Peronopsidae Westergård, 1936 Genus *Peronopsis* Hawle & Corda, 1847

Synonym. – Eoagnostus Resser & Howell, 1938 (see below). Robison (1964: 529) considered the following genera also to be synonyms of *Peronopsis; Mesospheniscus* Hawle & Corda, 1847, *Diplorrhina* Hawle & Corda, 1847, *Mesagnostus* Jaekel, 1909 and *Acadagnostus* Kobayashi, 1939. Robison (1994: 42), who takes a wide view of the content of the genus, listed the following genera as synonyms of *Peronopsis: Euagnostus* Whitehouse, 1936, *Archaeagnostus* Kobayashi, 1939, *Itagnostus* Öpik, 1979, *Svenax* Öpik, 1979, *Axagnostus* Laurie, 1990, *Eoagnostus* and *Mesagnostus*. Acadagnostus and *Micagnostus* Khajrullina in Repina *et al.* 1975 were considered to be questionable synonyms of *Peronopsis* by Robison (1994).

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

Remarks. – Resser & Howell (1938: 216) described the type species of *Eoagnostus, E. roddyi*, from flattened and poorly preserved material, and gave a short, inadequate, diagnosis of the genus. The characteristics of *Eoagnostus*, as given by Resser & Howell (1938), were that the glabella has only the posteroglabella developed, and the pygidium has a bluntly pointed axis. Rasetti & Theokritoff (1967) described a new species, *Eoagnostus acrorhachis*, from the Taconic Sequence of New York State. For this species they noted (p. 193) variation in the definition of the anteroglabella from ".... faintly defined, rounded in front, to entirely effaced." Rasetti & Theokritoff (1967) considered it to be plausible that



Fig. 13. *Peronopsis roddyi* (Resser & Howell, 1938). Henson Gletscher Formation. 1a, b, pygidium, internal mould, dorsal and lateral views, MGUH 23141 from GGU collection 298545, x 21. 2a, b, cephalon, internal mould, dorsal and lateral views, MGUH 23133 from GGU collection 298545, x 18. 3, complete specimen, dorsal view, MGUH 23127 from GGU collection 298545, x 20.5. 4, complete specimen, internal mould, dorsal view, MGUH 23126 from GGU collection 298545, x 20.5. 5, cephalon, dorsal view, MGUH 23130 from GGU collection 271750, x 17. 6, cephalon, internal mould, dorsal view, MGUH 23132 from GGU collection 298545, x 20.5. 7, cephalon, partially exfoliated, dorsal view, MGUH 23134 from GGU collection 298545, x 24. 8, cephalon, partially exfoliated, dorsal view, MGUH 23130, x 17.



Fig. 14. *Peronopsis roddyi* (Resser & Howell, 1938). Henson Gletscher Formation. 1a, b, cephalon, dorsal and lateral views, MGUH 23131 from GGU collection 271750, x 18. 2, complete specimen, latex of external mould, dorsal view, MGUH 23124 from GGU collection 298545, x 16. 3a, b, pygidium, internal mould, dorsal and lateral views, MGUH 23140 from GGU collection 298545, x 21. 4, complete specimen, internal mould, dorsal view, MGUH 23125 from GGU collection 298545, x 19. 5a, b, pygidium, dorsal view, MGUH 23125 from GGU collection 298545, x 17. 6a, b, cephalon, internal mould, dorsal and lateral views, MGUH 23135 from GGU collection 298545, x 26. 7a, b, pygidium, dorsal and lateral views, MGUH 23138 from GGU collection 298545, x 14.

Eoagnostus was closely related to early forms of *Peronopsis*, which first appear in the same strata, since ".... the cephalon is essentially identical" except for the effaced anteroglabella. The pygidia of the two genera were considered to be ".... not basically different". Their new species *E. acrorhachis* was considered to be essentially the same as *E. roddyi*. Due to poor preservation of the type material of *E. roddyi*, however, a new species was erected.

Following examination of the type material of both species, *E. roddyi* and *E. acrorhachis* are considered to

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be conspecific. In cephala figured by Rasetti & Theokritoff (1967) as *E. acrorhachis*, the anteroglabella varies from being clearly defined by a shallow furrow to totally effaced. This material is comparable to that from North Greenland and, from the study of this material, the variation in the degree of effacement of the anteroglabella is known to be considerable within a single population. A weakly defined, to effaced, anteroglabella is not considered to be a generically diagnostic feature, and *Eoagnostus* is synonymised with *Peronopsis*, as suggested also by Robison (1994). Diagnosis. – Emended from Robison (1964: 529, but see also Robison 1994: 42). Cephalon with well-defined posteroglabella. Glabella parallel-sided to gently tapered, usually bilobed although anteroglabella may be effaced. Preglabellar median furrow absent. Pygidium with welldefined axial furrow. Anteroaxis commonly parallel-sided, posteroaxis bluntly tapered. Lateral furrows shallow or absent. Axial node on M2. Axis rarely extends to border furrow. Postaxial furrow usually present.

Peronopsis roddyi (Resser & Howell, 1938)

Figs 13-16; 25.4,5,7

- 1938 Eoagnostus roddyi Resser & Howell, p. 216, pl. 3, figs 1-4.
- 1967 *Eoagnostus roddyi* Resser & Howell; Rasetti & Theokritoff, p. 193, pl. 20, figs 15-19.
- 1967 *Eoagnostus acrorhachis* Rasetti & Theokritoff, n. sp., p. 194, pl. 20, figs 1-14.
- 1967 Peronopsis sp. cf. P. primigenea (Kobayashi); Rasetti & Theokritoff, p. 195, pl. 20, figs 23-25.
- 1967 Peronopsis pygidium 1, Rasetti & Theokritoff, p. 196, pl. 20, figs 29-30.
- 1967 *Peronopsis* pygidium 2, Rasetti & Theokritoff, p. 196, pl. 20, figs 27-28.
- 1986 Peronopsis sp., Blaker, p. 70.
- 1994 Peronopsis roddyi, Robison 1994, p. 42.



Fig. 15. *Peronopsis roddyi* (Resser & Howell, 1938). Henson Gletscher Formation. 1, complete specimen, latex of external mould, dorsal view, MGUH 23128 from GGU collection 298545, x 16. 2a, b, cephalon, partially exfoliated, dorsal and lateral views, MGUH 23129 from GGU collection 271750, x 15.

Type material. – USNM 90796-90798 from the Lower Cambrian Kinzers Shale, near Lancaster, Pennsylvania, U.S.A.

Figured material. – Complete specimen; MGUH 23124-23128, 23281, 23282 from GGU collection 298545. Cephalon; MGUH 23129-23131, 23281, 23282 from GGU collection 271750, MGUH 23132-23135 from GGU collection 298545, MGUH 23136-23137 from GGU collection 315107. Pygidium; MGUH 23138-23139 from GGU collection 271750, MGUH 23140-23141 from GGU collection 298545, MGUH 23142-23143 from GGU collection 315107.

Other material. – GGU collections 271750, 298545 (abundant complete specimens), 315107.

Diagnosis. – Moderately convex (tr. & sag.) subquadrate cephalon with elongate glabella. Highly convex (tr.) posteroglabella slopes rapidly down to well-defined F3. F1 and F2 very weakly developed or absent. Anteroglabella of variable development from well-defined to effaced. Furrow defining anteroglabella well-developed to absent. Border without spines. Pygidial axis strongly convex (tr. & sag.), F1 and F2 poorly-defined. Axis does not reach to border furrow. Border without spines.

Description. - Cephalon subquadrate in outline, moderately convex transversely and longitudinally. Posteroglabella parallel-sided, or tapering gently forwards, defined anteriorly by well-impressed F3. F3 often shallows over sagittal line, and is variable from gently convex anteriorly, through to concave posteriorly. Width of glabella at F3 equal to, or slightly greater than, adjacent gena. Posteroglabella highly convex (tr.) at posterior, slopes strongly down to F3. Median node not apparent on posteroglabella. F1 and F2 of variable development, absent on many specimens. F2 may be represented by sharp contractions of the glabella sides and deepening of the axial furrow, rarely connected across glabella by very shallow furrow. F1 occasionally marked by a pit in the axial furrow, and very slight contraction of glabella sides. Posteroglabella defined by moderately deep and wide furrow. Anteroglabella of extremely variable development, showing complete range from total effacement to well-defined by narrow furrow. When defined, of variable outline, gently convex (tr. & sag.) and sloping gently down anteriorly. Sagittal length of anteroglabella one-third that of glabella. Basal lobes simple. Genae slope strongly outwards, and are of subequal transverse width. Border well-defined by deep furrow that is widest anterolaterally, narrowing considerably posteriorly. Wide, convex border, narrows rapidly posteriorly and lacks spines, though fulcral points prominent.

Thorax formed of two typical segments that are moderately convex transversely. Median axial lobe wide (tr.), approximately two-thirds width of segment. Lateral margins of medial axial lobe strongly convex outwards. An-



Fig. 16. *Peronopsis roddyi* (Resser & Howell, 1938). Henson Gletscher Formation. 1, pygidium, partially exfoliated, dorsal view, MGUH 23143 from GGU collection 315107, x 20. 2, pygidium, partially exfoliated, dorsal view, MGUH 23139 from GGU collection 271750, x 17. 3, cephalon, dorsal view, MGUH 23137 from GGU collection 315107, x 24.

terior and posterior pleural bands separated by short, deep, pleural furrow.

Pygidium subquadrate in outline, highly convex (tr. & sag.). Prominent axis about one-half width (tr.) of pygidium at its broadest. Axis strongly convex transversely, in lateral profile moderately convex and sloping rapidly down over posterior two-thirds. F1 and F2 poorly defined by contractions of axis, and short, diffuse furrows. Furrows barely apparent on some specimens. Axis tapers gently over anteroaxis, with slightly ogival posteroaxis narrowing rapidly to a bluntly rounded point. Axis does not reach to border furrow. Weakly developed axial node on M2, slightly elongated along sagittal line. Axial furrow deep and narrow. Postaxial median furrow developed on small specimens, particularly evident close to posterior of axis; very faintly defined or absent on large specimens. Pleural fields slope strongly downwards from axial furrow to border furrow, and are of equal transverse width. Border furrow wide and of moderate depth sagittally, narrowing anterolaterally. Border without spines, very gently convex, widest sagittally, narrowing anterolaterally to less than half maximum width.

When preserved sculpture consists of fine granules on the glabella and genae, pygidial axis and pleural fields.

Discussion. – As discussed above, *Eoagnostus roddyi* and *E. acrorhachis* were separated on account of differences in preservation by Rasetti & Theokritoff (1967), and the two are regarded as conspecific.

Cephala figured as *Peronopsis* sp. cf. *P. primigenea* (Kobayashi, 1939) by Rasetti & Theokritoff (1967) were found in association with the specimens that they assigned to *E. acrorhachis*; these seem to have been distinguished only on the well-defined anteroglabella, for in all other details of morphology they are identical. As a complete range of definition of the anteroglabella is now known from a single population, this criterion is no longer valid and these specimens are placed in synonomy with *Peronopsis roddyi*.

Associated with the cephala assigned to *Peronopsis* sp. cf. *P. primigenea* are two pygidia that Rasetti & Theo-

kritoff (1967) described as *Peronopsis* pygidium 1 and 2. *Peronopsis* pygidium 1 is comparable to the material of *Peronopsis roddyi* from North Greenland in all respects, and is considered synonymous. Pygidium 1 was considered by Rasetti & Theokritoff (1967) to differ from pygidium 2 in its dimensions and better development of the sagittal node on M2. The differences are only slight and occur within the range of morphology exhibited by the North Greenland material. The most notable difference is that pygidium 2 lacks a granular sculpture. This lack of granular sculpture is noted, however, on many pygidia from the larger North Greenland population, and pygidium 2 is also referred to the *P. roddyi*.

Peronopsis roddyi has similarities to Peronopsis amplaxis Robison, 1982 which was recorded from the Henson Gletscher Formation Middle Cambrian (Ptychagnostus gibbus Zone) by Robison (1982: 152). This species can be separated from P. roddyi in terms of relative convexity, in particular the posteroglabella of P. amplaxis is not strongly inflated, and the anteroglabella is always well-defined. The thorax of P. amplaxis also differs in that the medial axial lobes have developed lateral axial lobes. The pygidia share the subdued segmentation of the axis but the posteroaxis of P. amplaxis terminates closer to the border furrow, in many specimens reaching it. In view of the relative stratigraphic occurrences of P. roddyi and P. amplaxis, and the overall morphological similarities, it seems reasonable to suggest that P. amplaxis evolved from P. roddyi.

Occurrence in North Greenland. – Henson Gletscher Formation, collection localities 1 and 6 in Figs 8A, 10, 11. Age: Early Cambrian, *Olenellus* Zone.

Order uncertain Superfamily Eodiscoidea Richter, 1933

Diagnosis. – After Jell (1975: 26). Small trilobites with subequal cephalon and pygidium, and two or three thoracic segments. Glabella only reaches border furrow in a few blind genera; basal lobes generally absent; occipital furrow present in most genera, varies in degree of impression. Genae confluent or separated by longitudinal depression in front of glabella. Cephalic rim usually tapering posteriorly; smooth or bearing a row of tubercles, pits or radial scrobicules. Pygidium subtriangular to semicircular; long (sag.) axis unsegmented or have from 4 to 15 segments.

Remarks. – Howell (in Moore 1959) considered eodiscoids to be agnostoids, Jell (1975, see also Müller & Walossek 1987) thought eodiscids were ancestral to agnostids, while Robison (1987) considered their assignment doubtful. Babcock (1994a) recently reviewed the systematic position of the eodiscid trilobites, a group including characters common to both polymerids and agnostids. He concluded that the 6 eodiscid genera within his cladistic analysis seemed to be polyphyletic descendants of polymerid trilobites and that the eodiscid condition represented a grade of trilobite evolution as distinct from a clade. Babcock (1994a) noted that available evidence did not suggest that agnostids and eodiscids shared a close common ancestor.

Family Eodiscidae Raymond, 1913

Diagnosis. – After Jell (1975: 29). Glabella parallel-sided or tapering, generally not reaching anterior border furrow. Genal angles usually truncated. Occipital furrow usually discontinuous over axis. Cranidial spine usually present. Marginal cephalic spines absent. Genae posterolaterally inflated, not overhanging border laterally. Pygidial axis narrow (tr.), elevated above pleural areas.

Genus Calodiscus Howell, 1935

Synonyms. – Goniodiscus Raymond, 1913 (after Rasetti 1952), Brevidiscus Kobayashi, 1943 (after Rasetti 1952)

Type species. – By original designation; *Agnostus lobatus* Hall, 1847 (p. 258, pl. 57, figs 5a-f) from the Lower Cambrian West Castleton Formation in the Taconic region of New York State, U. S. A.

Diagnosis. – Eodiscid with glabella parallel-sided or tapering gently forwards. Glabella weakly trilobate with long (sag.) L2. S1 and S2 occasionally continuous across glabella. Occipital furrow moderately well-impressed, continuous over axial line. Cephalic border narrow, genal angles truncated. Pygidium semicircular in outline with up to six complete axial rings. Pleural fields normally furrowed, and pygidial margin frequently serrated.

Remarks on included species. – Jell (1975: 28) removed six species from the genus (C. chachlovi Fedyanina,

1962, *C. fissifrons* Rasetti, 1966a, *C. inflatus* Poletaeva, 1960, *C. nanus* Palmer, 1968, *C. reticulatus* Rasetti, 1966a and *C. theokritoffi* Rasetti, 1967), assigning them to a new unnamed genus of the Weymouthiidae Kobayashi, 1943. He reassigned these species on the basis that they are characterised by a strongly lobate glabella with one or two very deep transglabellar furrows, an expanded and bulbous posterior lobe and poorly impressed occipital furrow. The pygidial axis is formed of seven or more rings. Öpik (1975) named the genus *Meniscuchus*, and also included *C. helena* of Lazarenko (1964) which he suggested may be the senior synonym of *C. fissifrons* and *C. reticulatus. Calodiscus granulosus* Egorova & Schabanov, 1972 in Savitsky *et al.* (1972) is here transferred to *Meniscuchus*.

Calodiscus lobatus (Hall, 1847)

Fig. 17

- 1847 Agnostus lobatus Hall, p. 258, pl. 57, figs 5a-f.
- 1977 Calodiscus korolevi Pokrovskaya sp. nov., in Ergaliev et al., p. 20, pl. 1, figs 1-3.
- 1984 *Calodiscus lobatus* (Hall, 1847); Ahlberg, p. 352, figs 3a-k, 4a-e (includes synonomy).
- 1993 Calodiscus lobatus (Hall, 1847); Ahlberg & Bergström, p. 331, fig. 1 (includes synonymy).

Type material. – Lower Cambrian West Castleton Formation in the Taconic region of New York State, U. S. A.; it was redescribed by Rasetti (1952) and is held at the American Museum of Natural History (AMNH 210).

Figured material. – Cephalon; MGUH 23144-23150 from GGU collection 315049. Pygidium; MGUH 23151-23153 from GGU collection 315049.

Other material. - GGU collection 315049 (abundant).

Diagnosis. – Glabella conical, tapering gently forwards, two pairs of glabellar furrows. S1 and S2 continuous across glabella, defining long (sag.) L2. Low ocular ridges close to anterior margin of gena. Pygidial pleural fields furrowed, axis of four or five rings, irregular border with up to three pairs of short spines.

Description. – Cephalon gently convex (tr. & sag.), subquadrate in outline with maximum transverse width greater than sagittal length. Glabella moderately convex transversely, in lateral profile horizontal over posterior half, anteriorly sloping gently downwards to anterior border furrow. Glabella tapers moderately forwards between SO and S1, then more gradually anteriorly of S1 with strongly rounded anterior. Glabella with overall conical, or subconical outline. Glabella reaches to anterior border furrow, or is separated from it by very short (sag.) pregla-

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Fig. 17. *Calodiscus lobatus* (Hall, 1847). Kap Troedsson Formation. 1, cephalon, internal mould, dorsal view, MGUH 23146, x 19. 2, cephalon, internal mould, dorsal view, MGUH 23146, x 19. 3, cephalon, internal mould, dorsal view, 23147, x 20. 4, cephalon, partially exfoliated, dorsal view, MGUH 23150, x 20. 5, cephalon, internal mould, dorsal view, MGUH 23144, x 18. 6, cephalon, internal mould, dorsal view, MGUH 23148, x 18. 7, cephalon, internal mould, dorsal view, MGUH 23145, x 20. 8, pathological pygidium, internal mould, dorsal view, MGUH 23151, x 24. 9, pygidium, internal mould, dorsal view, MGUH 23152, x 24. All specimens from GGU collection 315049.

bellar field. Two pairs of lateral glabellar furrows on some specimens, only a single pair apparent on others. S1 shallow and continuous across glabella, reaches to axial furrow; variable from straight to gently concave posteriorly. S2 very faintly defined, transverses glabella and reaches to axial furrow. L2 up to twice as long (sag.) as L1, and of about equal length to the anterior glabellar lobe. Axial furrow of moderate width (tr.) and depth, shallowing slightly anteriorly. Occipital furrow of moderate depth and variable width, continuous across glabella and gently concave posteriorly. Occipital ring slightly wider (tr.) than glabella across L1, with strongly curved posterior margin. Occipital ring moderately convex (tr.) without spine or node. Sagittal length of occipital ring between one-fifth and one-quarter that of glabella. Gena as wide, or slightly wider than, glabella at midpoint. Ocular ridges very low, gently curved and situated close to anterior margin of genae. Border furrow wide and deep sagittally, narrowing and shallowing anterolaterally, being at its narrowest laterally, then widening posterolaterally. Cephalic border very gently convex, narrowest laterally, attaining maximum width (sag.) in front of glabella. Border without nodes or tubercles. Posterior border furrow wide (exsag.), curved moderately anterolaterally, and confluent with lateral furrow. Posterior border short (tr.), widening distally to prominent fulcrum.

Pygidium moderately convex (tr. & sag.) with sagittal length approximately four-fifths maximum transverse width. Prominent axis tapers gently posteriorly and reaches to posterior border furrow. Anteriorly axis occupies one-half the width between prominent fulcra. Four or five axial rings and a very short terminal piece form axis. Inter-ring furrows narrow and deep. Axial rings without median nodes or spines. In lateral profile axis averages horizontal over anterior three rings, posteriorly sloping down strongly to border furrow. Axial furrow narrow and of moderate depth. Narrow (tr.) pleural fields slope down strongly to border furrow and are crossed by three pairs of distinct pleural furrows that reach to the border furrow. A fourth pair of pleural furrows barely apparent on some specimens. Very faint interpleural furrows on all pleura. Anterior pleural strip of first pygidial segment with fulcrum at about one-third distance from axial furrow to lateral border. Border furrow narrow and of medium depth throughout. Border wider than furrow, gently convex and at its widest posterolaterally. Anterolaterally border irregular with two or three pairs of short spines. All parts of the exoskeleton without apparent sculpture. A single specimen is pathogenic with the anterior two axial rings being affected (see Fig. 17.8).

Discussion. – As discussed by Ahlberg (1984: 355), *Calodiscus lobatus* is a variable species particularly in the shape of the glabella and the development of its lobation. Additionally, sculpture varies from being absent to a dense cover of granules over all parts of the exoskeleton.

The material from North Greenland differs from the type material of *C. lobatus* in the retention of vestigial ocular ridges but this is not considered to be sufficient basis on which to distinguish a separate taxon, particularly in view of the variability of the species.

Calodiscus korolevi Pokrovskaya (in Ergaliev et al. 1977) is known only from incomplete pygidia. The three figured specimens share with C. lobatus an axis with four or five rings and narrow (tr.) pleural fields crossed by three pairs of pleural furrows. The morphology of C. korolevi lies within the range of variability of C. lobatus and the two are regarded as conspecific.

Cephala of *C. lobatus* from North Greenland are also similar to the holotype cephalon of *Calodiscus meeki* (Ford, 1876) from the Lower Cambrian Schodack Formation (now West Castleton Formation) of the Taconic Sequence of New York State, figured by Rasetti (1952, pl. 51, fig. 19). The North Greenland specimens of *C. lobatus* differ primarily in the lack of both granular sculpture and faint nodes on the lateral parts of the border, although it is of note that granular sculpture was recorded by Ahlberg (1984) on material of *C. lobatus* from Jämtland, Sweden. As discussed by Rasetti (1952: 442), in the absence of a pygidium of *C. meeki*, the holotype cranidium could be assigned to *Serrodiscus*, but cephalic morphology is closer to that of *Calodiscus*. In view of these uncertainties it is suggested that *Calodiscus meeki* be restricted to the type specimen.

In addition to material described here, *Calodiscus* was reported from the basal beds of the Aftenstjernesø Formation by Christie & Peel (1977; see also Palmer & Peel 1979).

Occurrence in North Greenland. – Aftenstjernesø Formation. Kap Troedsson Formation, collection locality 4 in Figs 6 and 7. Age: Early Cambrian, *Olenellus* Zone.

Genus Ekwipagetia Fritz, 1973

Type species. – By original designation; *Ekwipagetia plicofimbria* Fritz, 1973, p. 10, pl. 6, figs 1-24, from the medial Lower Cambrian, Mackenzie Mountains, Northwest Territories, north-western Canada.

Emended diagnosis. – Eodiscid with cranidial spine, extending posteriorly and dorsally. Poorly segmented glabella. Anterior border with epiborder furrow, scrobicules not developed. Narrow, deep palpebral furrows; wide (tr.) palpebral lobes. Bacculae not developed. Pygidium with axis of four to six rings, separated from border by short (sag.) connective band. Pronounced axial spine originates from variable position, rarely terminal. Interring furrows very shallow or absent. Nodose pygidial border.

Remarks. - The similarities between Pagetia and Ekwipagetia were discussed by Jell (1975: 16). He considered each of the main diagnostic features of Ekwipagetia as given by Fritz (1973) and noted that for Ekwipagetia the epiborder furrow is only slightly better impressed than in some species of Pagetia (e.g. P. silicunda Jell, 1975), and that nodose and serrated pygidial margins are also known in Pagetia (e.g. P. howardi Jell, 1975) Jell also considered that the lack of border scrobicules in Ekwipagetia was not generically significant. Fritz (1973: 9) had also included in the diagnosis of *Ekwipagetia* that this is a "Pagetiid of greater than average size". As pointed out by Jell (1975), however, several species of Pagetia such as P. edura, P. silicunda and P. oepiki (all Jell, 1975) are of similar or greater size than specimens of Ekwipagetia.

An additional similarity noted by Jell (1975) was that *Ekwipagetia* has a terminal axial spine. In *Pagetia* the spine is consistently at the terminus of the axis. Although the figured pygidia of *Ekwipagetia plicofimbria* in Fritz (1973) have terminal axial spines, the type material includes many specimens in which the spine originates from the posterior axial ring, a condition that is not



Fig. 18. *Ekwipagetia marginata* (Rasetti, 1967). Kap Troedsson Formation. 1a, b, cranidium, internal mould, dorsal and latefal views, MGUH 23158 from GGU collection 315051, x 12. 2a, b, pygidium, internal mould, dorsal and lateral views, MGUH 23166 from GGU collection 315145, x 15. 3a, b, pygidium, internal mould, dorsal and lateral views, MGUH 23165 from GGU collection 315145, x 13. 4a, b, pygidium, partially exfoliated, dorsal and lateral views, MGUH 23163 from GGU collection 298984, x 14. 5a, b, cranidium, partially exfoliated, dorsal and lateral views, MGUH 23159 from GGU collection 315145, x 9. 6a, b, pygidium, internal mould, dorsal and lateral views, MGUH 23167 from GGU collection 315145, x 15.

known in *Pagetia*. As is discussed below, in populations of *Ekwipagetia marginata* (Rasetti, 1967) from North Greenland, the pygidial spine is not known to originate from the terminus, but rather from the posterior axial ring(s). It was concluded by Jell (1975: 18) that "... there is no clear demarcation between the two genera".

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Clearly, the two genera are very closely related although they appear to be separable on the position of pygidial spine origination. However, as the two species assigned to *Ekwipagetia* are older than any assigned to *Pagetia*, and there is variation in spine position both within, and between, the two species, it could be argued that stability in the position at which the spine originates was not established until the late Early Cambrian (the age of the oldest specimens presently assigned to *Pagetia*), and that *Ekwipagetia* should be regarded as a synonym of *Pagetia*. Although these genera are similar, it is considered here that they can be differentiated on a combination of the characters given in the diagnosis.

Jell (1975) concluded that *Ekwipagetia* was an early representative of the *Pagetia* lineage. This appears to be a reasonable evolutionary relationship, and one which corresponds to the age data available on both genera. It appears, however, that the time interval between *Ekwipagetia* and *Pagetia* may not be as great as was envisaged by Jell (1975). Fritz (1973) considered *Ekwipagetia* to be of *"Nevadella"* Zone age in north-western Canada, with *Pagetia* first appearing in the late *Olenellus* Zone. However, he also reported occurrences of *Ekwipagetia* spp. from the *Olenellus* Zone, only 100 km from the type locality of *Ekwipagetia*.

The material from North Greenland is of undoubted Olenellus Zone age; it is suggested that Ekwipagetia was present in the early to middle *Olenellus* Zone in North Greenland, with *Pagetia* appearing in the late *Olenellus* Zone.

Ekwipagetia marginata (Rasetti, 1967)

Figs 18; 19; 20.1,2,4,5

- 1967 Hebediscus marginatus Rasetti, p. 67, pl. 6, fig. 19.
- 1979 cf. *Hebidiscus marginatus* Rasetti; Hurst & Peel, p. 43.

Type material. – Type material is deposited at the Natural History Museum, Smithsonian Institution, Washington D. C., U.S.A. Holotype cranidium (USNM 156637) from a limestone lens in black shale about one mile east of Salme, Washington County, New York State.

Figured material. – Cranidium; MGUH 23154 from GGU collection 271505, MGUH 23155 from GGU collection 298982, MGUH 23156 from GGU collection 298984, MGUH 23157-23158 from GGU collection 315051, MGUH 23159-23160 from GGU collection 315145. Pygidium; MGUH 23161 from GGU collection



Fig. 19. *Ekwipagetia marginata* (Rasetti, 1967). Kap Troedsson Formation. 1a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23156 from GGU collection 298984, x 15. 2a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23155 from GGU collection 298982, x 12. 3, pygidium, internal mould, dorsal view, MGUH 23164 from GGU collection 315145, x 15. 4, pygidium, internal mould, dorsal view, MGUH 23161 from GGU collection 270505, x 17.





1,2,4,5. *Ekwipagetia marginata* (Rasetti, 1967). 1, cranidium, internal mould, dorsal view, MGUH 23154 from GGU collection 270505, x 14. 2, pygidium, internal mould, dorsal view, MGUH 23162 from GGU collection 298982, x 15. 5, cranidium, partially exfoliated, dorsal view, MGUH 23157 from GGU collection 315051, x 11. 4, cranidium, internal mould, dorsal view, MGUH 23160 from GGU collection 315145, x 10.

3. Kootenia sp. B. Pygidium, internal mould, dorsal view, MGUH 23446 from GGU collection 315051, x 8.

6a, b. Labradoria misera? (Billings, 1861). Cranidium, lateral and dorsal views, MGUH 23595 from GGU collection 270505, x 12.

270505, MGUH 23162 from GGU collection 298982, MGUH 23163 from GGU collection 298984, MGUH 23164-23167 from GGU collection 315145.

Other material. – GGU collections 270504, 270505, 298982-298984, 315049, 315051, 315145 (abundant).

Diagnosis. – Species of *Ekwipagetia* with pygidial axis of four or five rings. Long (sag.), narrow (tr.) glabella separated from anterior border by wide (sag.) furrow. Epiborder furrow of constant depth throughout.

Description. – Exclusive of occipital spine, cranidium subquadrate in outline; moderately convex transversely and longitudinally. Prominent glabella tapers forward, strongly rounded at the anterior. Transversely glabella moderately convex, in lateral profile gently convex over the posterior half, with anterior half sloping rapidly downwards to preglabellar furrow. Two pairs of glabellar

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furrows which are barely apparent on many specimens. S1 short, diffuse and shallow, directed moderately backwards and situated at approximately two-fifths glabellar length. S2 at adaxial termination of ocular ridges, very short and directed backwards at more obliquely than S1. Axial furrow broad (tr.) and deep posteriorly, with reduction in both width and depth anteriorly; confluent with very narrow preglabellar furrow. Anterior border furrow very wide (sag.) and of medium depth in front of glabella, narrowing distally. Sagittal length of border furrow variable between one-quarter and one-third that of the glabella (excluding occipital ring). Strongly convex (tr.) occipital ring defined distally by short, deep incisions that are directed strongly backwards, with SO not continuous across glabella on most specimens. Sagittally, L1 and occipital ring extend backwards into long, slender cranidial spine directed dorsally and posteriorly. Anterior border wide (sag.), narrowing distally, sagittal length approximately one-quarter that of glabella. Epiborder furrow of medium depth that parallels the margin and divides the border into two parts of about equal sagittal length. Epiborder furrow very weakly developed, or not apparent on smallest cranidia. Palpebral areas asymmetrically convex (tr.), sloping moderately inwards towards axial furrow. Palpebral area arises abruptly from posterior border and anterior border furrow, more gradually from axial furrow. Transverse width of palpebral areas about equal to basal glabellar width. Wide (tr.) palpebral lobes set below level of fixed cheek. Lobes gently cresentic and defined by narrow, long (exsag.) and deep furrow. Exsagittal length of lobes approximately one-third that of glabella, and centred just posteriorly of glabella midlength. Ocular ridges of low relief, very gently curved and defined by change in slope of exoskeleton. Posterior border furrow deep and gently curved anterolaterally, widening distally. Posterior border narrow and directed gently posterolaterally over adaxial two-thirds, with distal third gently downturned. Anterior section of facial suture straight, strongly divergent at about 80 degrees to an exsagittal line. Posterior section very short, straight and transverse.

Pygidium semicircular in outline; axis very gently convex (tr.), tapering gradually posteriorly, separated from posterior border furrow by a very short (sag.) connective band. Anteriorly, axis occupies approximately two-fifths the transverse width between two prominent fulcra. Axis formed of four axial rings, with a fifth ring weakly developed on larger specimens, and a long (sag.) terminal piece. Anteriorly axis defined by narrow (tr.), deep furrow with reduction in both width and depth posteriorly. Axial rings defined by deep, short lateral notches that are occasionally continuous across the axial line where they are considerably shallower. Large axial spine developed on fourth axial ring; on some specimens spine base also incorporates posterior of third ring, and more rarely entire third ring. Spine not consistently centred, but often positioned laterally to sagittal line; it appears to have been stout and directed strongly upwards and backwards. In lateral profile axis slopes rapidly downwards posteriorly of spine base, whilst anteriorly axis is on average horizontal. Pleural fields crossed by weak impressions of three pairs of pleural furrows on most specimens, although four and five pairs are discernible on some larger pygidia. Very faint impressions of one or two pairs of interpleural furrows are developed on some specimens. Border furrow of medium depth anteriorly, narrowing and increasing in depth posteriorly. Border flat to very gently convex, narrow and bearing up to five pairs of short border spines whose spacing decreases posteriorly. In lateral profile the border often has a distinctly stepped appearance (see Fig. 18.3b). On some specimens these spines are incipient, appearing only as nodes. Sculpture has only been observed on a few pygidia and consists of fine granules on the pleural fields and axis; on the axis there appears to be a degree of longitudinal alignment of the granules.

Discussion. – Rasetti (1967) referred a single cranidium to his new species *Hebediscus marginatus* from Lower Cambrian strata of the Taconic Sequence, Washington County, New York State. The similarity of the present material to *H. marginatus* was previously noted by Hurst & Peel (1979: 43).

The inclusion of Hebediscus marginatus Rasetti, 1967 in Ekwipagetia had earlier been suggested by Fritz (1973) with doubt as it was known only from the single cranidium. The type specimen can now be positively assigned to *Ekwipagetia* since it falls within the variation range shown by large populations of this species from North Greenland. Ekwipagetia marginata differs from the type species, E. plicofimbria (see Fritz 1973, pl. 6, figs 5, 9), in the relatively longer (sag.) and narrower (tr.) glabella which is highly convex in lateral profile over the posterior two-thirds. The glabella of E. marginata either slopes slightly anteriorly or is gently convex. Fritz (1973: 10) also described the glabella of E. plicofimbria as "... reaching short distance into anterior border furrow.", whilst for E. marginata the glabella does not extend beyond the level of the gena, and for many specimens the left and right gena are confluent. Also in the Canadian specimens of E. plicofimbria S2 is directed slightly forward, as opposed to backwards for the Greenland material of E. marginata. In larger cranidia of E. plicofimbria the epiborder furrow is barely apparent over the sagittal line, whilst on the North Greenland material there is no reduction in depth over any part of the epiborder furrow.

Occurrence in North Greenland. – Kap Troedsson Formation, collection localities 1-4 in Figs 6 and 7. Age: Early Cambrian, *Olenellus* Zone.

Genus Pagetides Rasetti, 1945

Synonyms. – *Neopagetina* Pokrovskaya in Chernysheva 1960. *Discomesites* Öpik, 1975 (see below).

Type species. – By original designation; *Pagetides elegans* Rasetti, 1945 from the Lower Cambrian Ville Guay Conglomerate, Quebec, Canada.

Diagnosis. – Emended from Rasetti (1945). Small, isopygous, proparian trilobites. Narrow (tr.) glabella with two pairs of furrows. Posterior glabellar lobe and occipital ring extended into cranidial spine. Short (exsag.), narrow palpebral lobes; ocular ridges indistinct. Extremely small free cheeks. Semicircular pygidium with narrow (tr.) axis not reaching posterior border furrow. Axis of up to seven rings, without terminal spine. Narrow border without spines.

Remarks. – Which eodiscid species should be assigned to *Pagetides* and which to *Neopagetina* is a problem that

has existed for over forty years. Few Soviet workers have referred eodiscid species to *Pagetides*; all relevant Siberian material has been placed in *Neopagetina*, to which also has been referred the Australian Middle Cambrian *Pagetia significans* (Etheridge, 1902) and the North American, Early Cambrian *Neopagetina taconica* Rasetti, 1967. The similarities of *Pagetides* and *Neopagetina* were discussed by Rasetti (1966b). He restricted the latter genus to the type species *N. rjonsnitzkii* (Lermontova, 1940), and he referred to *Pagetia* Walcott, 1916 all other species which had previously been assigned to *Neopagetina*.

In the opinion of Palmer (1968: B33) the principal characteristics of Neopagetina, as used by Soviet palaeontologists, are "the presence of pleural furrows on the pygidium and an occipital spine on the cranidium. A terminal or subterminal axial spine on the pygidium may be present or absent." He believed that Pagetides had been used for species with nearly smooth pygidial pleural fields, an occipital spine (which therefore occurs in both "genera") and no axial pygidial spines. He further outlined the problems of adhering to this classification with regard to three new species which he described from the Lower Cambrian of Alaska. Of these species, all of which were known from very few specimens, two were considered to be closely related. These two species occurred in two different limestone clasts in the same limestone conglomerate at the same locality; they differ only in the degree of effacement of the pygidial pleural furrows and are probably synonymous. However, in terms of the then accepted classification, the more effaced species (P. occidentalis) would be referred to Pagetides whilst P. appolinis would be referred to Neopagetina. Palmer concluded, therefore, that Soviet workers placed too much importance on the development of pygidial pleural furrows, and had included in Neopagetina a variety of "possibly unrelated forms". He also removed four species (significans Etheridge, 1902, glabrata Lermontova, 1940, orbiculata and venusta both Lazarenko, 1962) from Neopagetina and assigned them to Pagetia for all four have "terminal or subterminal axial spines, are morphologically very similar to typical species of Pagetia and might better be placed in that genus." Hence, it was his conclusion that this "leaves only the degree of development of the pleural furrows as a criterion for discriminating Neopagetina from Pagetides". As was pointed out by Palmer (1968), however, Rasetti (1966b: 503) had previously doubted the validity of this criterion for taxonomic discrimination even at the specific level. This opinion is supported here since effacement is a common trend in almost all groups of trilobites. Palmer (1968) additionally noted that no characters of the cranidia of species referred to Pagetides and Neopagetina allow consistent discrimination of the two genera. In spite of all these conclusions he still only questionably synonymised the two genera.

Palmer (1972: D11) returned briefly to this problem with reference to a new species which he assigned to *Pagetides*? from the late Middle Cambrian of Antarctica, maintaining his position of 1968. Fritz (1972: 8), in describing Early Cambrian trilobites from north-west Canada tentatively retained *Neopagetina* as a separate genus concluding only that "... until *Neopagetina* is better known its position is difficult to assess".

Jell (1975) agreed with Rasetti (1966b) in maintaining Neopagetina and restricting it to the type species. He reasoned that as Pagetia is one of only two eodiscid genera possessing a terminal axial spine on the pygidium (the other is Helepagetia Jell, 1975), those species from Siberia with a terminal pygidial spine should be included in Pagetia. Jell considered Neopagetina to be characterised by "... a short (sag.) cephalic border without scrobicules, well impressed occipital furrow, very small free cheeks, large almost quadrangular pygidium, pygidial axis finishing well in front of the border furrow and no terminal axial spine." He pointed out that the illustrations of the type series of Neopagetina do not show clearly if there is a cranidial spine developed and, as such, this character should not be used to diagnose the genus. However, a cranidial spine is developed in North Greenland material of specimens assigned here to Pagetides rjonsnitzkii and this character is included in the diagnosis.

Öpik (1975) also reviewed Pagetides and Neopagetina. Öpik's (1975: 32) opinion was to maintain Neopagetina, diagnosing it has having "... a narrow cephalic rim, ribbed and furrowed pygidial pleural lobes, a long and multiannulated pygidial axis with median (axial) nodes, and a spineless terminus." He considered as diagnostic of Pagetides "(1) the cephalic rim is convex crescentic, widest and swollen in front and very narrow on the flanks; (2) a terminal axial spine is absent in the pygidium; (3) the pygidial axis is long, slender, and multisegmented; and (4) the pygidial pleural lobes are smooth, without ribs." In addition to the type species, he included the North American Neopagetina taconica Rasetti, 1967 and N. granulosa Palmer, 1968, presumably on the basis of well-defined pygidial pleural furrows in both. In addition, the Siberian species N. primaeva (Lermontova, 1940) was maintained, although N. orbiculata and N. venusta (both Lazarenko, 1962) were thought to be close to Pagetia, in agreement with Palmer (1968) and Jell (1975).

Jell (1975: 72) erected Macannaia (type species Macannaia maladensis (Resser, 1939) from Middle Cambrian strata at Two Mile Canyon, Malad, Idaho). Amongst the diagnostic characters he particularly referred to the "minimal development" of the pygidial terminal axial spine. Earlier Palmer (1972: D11) had allowed some development of an axial pygidial spine to characterise species of Pagetides, but stated that this development should not be significant. Agreement is expressed with Jell (1975) that Pagetides should be diagnosed as not having this spine developed. Indeed, one of the major distinctions between species of Pagetia and Pagetides is the presence or absence of a terminal axial pygidial spine. When there is minimal development of a spine, as in species described by Lazarenko (1959) from Siberia, it is obvious that difficulties of generic placement arise. The solution proposed by Jell (*i.e.* the erection of *Macannaia*) is supported, for in addition, species referred to that genus can be separated on a narrow (tr.) truncated glabella and a posterior border furrow that reaches the axial furrow.

Further disagreement between Jell (1975) and Öpik (1975) concerned *Pagetia latilimbata* Chien, 1961, a Middle Cambrian species from the Duliujiang Formation of south-west China. Öpik (p. 31) assigned the species to *Pagetides* while Jell retained the species in *Pagetia*. Again the conflict is based on the presence, or absence, of a terminal pygidial spine. Although the original illustrations are poor, the type material was refigured by Lu *et al.* (1965, pl. 6, figs 12, 13) and from these it is clear that the pygidial axis does not have an axial spine. Öpik's (1975) assignment of this species to *Pagetides* is therefore supported.

From the above account it is evident that the concepts of *Pagetides* and *Neopagetina* are far from clear with different workers placing emphasis upon different features. The new material from North Greenland allows identification of specimens referable to both type species from the same locality. The main argument of previous authors for not synonymising the two genera has been



Fig. 21. *Pagetides elegans* Rasetti, 1945. Henson Gletscher Formation. 1, cranidium, partially exfoliated, dorsal view, MGUH 23168 from GGU collection 225709, x 7. 2, cranidium, partially exfoliated, dorsal view, MGUH 23173 from GGU collection 298553, x 12.5. 3, pygidium, partially exfoliated, dorsal view, MGUH 23180 from GGU collection 218681, x 20. 4a, b, pygidium, internal mould, dorsal and lateral views, MGUH 23187 from GGU collection 315110, x 17. 5, pygidium, internal mould, dorsal view, MGUH 23188 from GGU collection 315110, x 21. 6, cranidium, partially exfoliated, dorsal view, MGUH 23185 from GGU collection 298553, x 12.7, pygidium, partially exfoliated, dorsal view, MGUH 23185 from GGU collection 298553, x 14.5. 8, pyg-idium, internal mould, dorsal view, MGUH 23186 from GGU collection 298553, x 15.


Fig. 22. *Pagetides elegans* Rasetti, 1945. Henson Gletscher Formation. 1, pygidium, internal mould, dorsal view, MGUH 23181 from GGU collection 225712, x 17. 2, pygidium, internal mould, dorsal view, MGUH 23182 from GGU collection 225712, x 22. 3, cranidium, partially exfoliated, dorsal view, MGUH 23169 from GGU collection 225709, x 15. 4a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23175 from GGU collection 298553, x 12. 5a, b, pygidium, partially exfoliated, dorsal and GGU collection 225714, x 17. 6, cranidium, internal mould, dorsal view, MGUH 23176 from GGU collection 225714, x 17. 6, cranidium, internal mould, dorsal view, MGUH 23176 from GGU collection 225714, x 17. 6, cranidium, internal mould, dorsal view, MGUH 23176 from GGU collection 298553, x 11.5. 7, pygidium, partially exfoliated, dorsal view, MGUH 23179 from GGU collection 218681, x 15.5.

that holaspids of species of *Pagetides* lack pygidial pleural furrows. However, the material described below shows that this is not the case, and suggests sufficient evidence to regard *Neopagetina* as a junior synonym of *Pagetides*.

Öpik (1975) described *Discomesites* from the Early Cambrian Cymbric Vale Formation of New South Wales, Australia, as having similarities to both *Pagetides* and *Neopagetina*. His new genus was differentiated from *Neopagetina* by its wider (sag.) cephalic border with median expansion and by its unfurrowed pygidium.

The morphology of the anterior border in this group of

trilobites is known to be very variable, and can not be used as a generic level character. This was shown by Palmer (1968) who noted that of the 14 species assigned to *Pagetides* only eight have a medial expansion of the cephalic border, three do not, and this feature is not obviously developed in the remaining three. Additionally, the state of effacement of the pygidial pleural furrows is also variable. Now that *Neopagetina* and *Pagetides* are considered to be synonyms, *Discomesites* falls within the emended diagnosis of *Pagetides* in terms of both of these morphological characters and is therefore a further junior subjective synonym.

Pagetides elegans Rasetti, 1945

Figs 21-23; 25.1

- 1945 Pagetides elegans Rasetti, n. sp., p. 313, pl. 1, figs 15-18.
- 1948 Pagetides elegans Rasetti; Rasetti, p. 11, pl. 1, figs 1-7.
- 1967 Pagetides elegans Rasetti; Rasetti, p. 64, pl. 5, figs 16-24.
- 1967 Neopagetina taconica Rasetti, p. 66, pl. 6, figs 20-28.

Type material. – Type series Laval University, Quebec, Canada 304a-c from the Lower Cambrian "Sillery Formation" near Lévis, Quebec, Canada.

Figured material. – Complete enrolled specimen; MGUH 23189 from GGU collection 298553A. Cranidium; MGUH 23168-23169 from GGU collection 225709, MGUH 23170-23172 from GGU collection 225714A, MGUH 23173-23176 from GGU collection 298553. Thoracic segment; MGUH 23177-23178 from GGU collection 225714A. Pygidium; MGUH 23181-23180 from GGU collection 225714, MGUH 23184, MGUH 23181-23182 from GGU collection 225714, MGUH 23184 from GGU collection 225714A, MGUH 23185-23186 from GGU collection 298553, MGUH 23187-23188 from GGU collection 315110. Meraspid pygidium; MGUH 23190 from GGU collection 225714A.

Other material. – GGU collections 218681, 225709, 225712, 225714, 271486, 298553, 301346, 301349, 315110 (abundant), 315110A (abundant), 315112.

Diagnosis. – Strongly depressed and broad (tr.) preglabellar field. Wide (exsag.) anterior border with median expansion. Glabellar furrows generally weakly impressed, not connected across glabella. Pygidium with axis of six or seven rings, nodes on at most anterior five rings. Pleural fields with up to six pairs of pleural furrows of moderate impression, or effaced.

Remarks. – The original description of *P. elegans* given by Rasetti (1945) is brief; a more complete description is given here based on the material from North Greenland.

Description. – Cranidium subquadrate in outline, moderately convex (tr. & sag.). Glabella tapers very gently forwards, strongly rounded anteriorly. Glabella of moderate transverse convexity, whilst in lateral profile it slopes gently downwards from occipital ring to level of S2, then more rapidly down to preglabellar furrow; defined laterally by broad (tr.) furrows that are deep anteriorly, shallowing slightly posteriorly. Axial furrows continuous with deep preglabellar furrow. S1 placed slightly forwards of midlength, formed by elongated pits adjacent to axial furrow, directed moderately backwards. S2 less distinct, of similar configuration. SO formed distally of deep, short furrows, directed strongly backwards and not joined across glabella. Posterior glabellar lobe and occipital ring extend backwards into stout cranidial spine, with sagittal length about one-half that of glabella. Preglabellar field well-developed sagittal length approximately one-quarter that of glabella. Anterior border wide (exsag.), moderately convex, with medial expansion of variable development. Frequently border displays moderately deep incisions that do not reach the border furrow, and have varying lengths and widths (see Fig. 22.4a). Border defined by furrow of moderate width (exsag.), deep distally with shallowing around medial expansion. Fixed cheeks strongly convex (tr.), rising steeply from the axial furrow and posterior border, rather more gently from the anterior border, and almost vertically from the free cheek to the rather flat tops. Gently arcuate palpebral lobes defined by straight, narrow (tr.) furrow. Length (exsag.) of lobes about one-third sagittal glabellar length; centred at midlength of L2. Very faint ocular ridges only evident on internal moulds. Width (tr.) of palpebral area approximately equal to that of occipital ring. Posterior border narrow (exsag.) adaxially with gradual widening distally, continuous with narrow (tr.) lateral border. Posterior border directed weakly posterolaterally, and defined by furrow that is curved gently to moderately anterolaterally. Border furrow very shallow adaxially, with increasing depth and width distally. Anterior section of facial suture straight, strongly divergent at angle of about 75 degrees to an exsagittal line. Posterior section straight and transverse.

Pygidium approximates to a semicircular outline, moderately convex transversely, in lateral profile gently convex anteriorly of fourth ring, posteriorly sloping strongly downwards. Axis formed of six complete rings and terminal piece, tapers gradually backwards and does not reach border furrow. Occasionally a weakly defined seventh ring is evident. Inter-ring furrows straight, transverse, anterior four generally of greater depth. Axial nodes may be present on up to the anterior five rings though these may be lacking on some specimens. Axial furrows shallow and narrow posteriorly, being faintly defined around the posterior of the axis. Short (sag.) connective band, steeply inclined, being almost vertical in some specimens. Pleural fields gently convex (tr.), transversed by up to six pairs of shallow pleural furrows. For small (<3 mm in sagittal length) specimens the anterior pair of pleural furrows are the most strongly impressed. For larger specimens all pairs are of about equal development, being deepest adaxially and very faint or absent abaxially. Pleural furrows more distinct on internal moulds. Interpleural furrows very faintly defined or absent. Border widest anterolaterally, narrowing to about half maximum width posteriorly, gently convex and defined by narrow furrow that shallows anterolaterally.

All parts of exoskeleton apparently lacking sculpture. Discussion. - Rasetti (1967) compared the cranidium of his N. taconica with that of Pagetides elegans Rasetti, 1945. The features that Rasetti (1967) gave as being distinct, are in fact known to be highly variable within the populations of P. elegans from North Greenland. For example, he cited that glabellar furrows are almost indistinct for P. elegans; a comparison of Fig. 21.6 and Fig. 22.6 from the same sample shows the extremes of development that occur. Rasetti (1967) did not compare pygidia, possibly because of the development of pleural furrows in N. taconica. As has already been discussed, however, pygidia of P. elegans from North Greenland have various degrees of effacement (see Fig. 21.5 and Fig. 22.2, 7). Differences in the depth of these furrows do not warrant distinction at the species level and, as the pygidia are comparable in all other details of morphology, N. taconica is considered to be a synonym of P. elegans.

Rasetti (1967) also compared his new species *Neopag*etina taconica with *Neopagetina rjonsnitzkii* (Lermontova, 1940), differentiating *N. taconica* by better defined palpebral lobes, lack of ocular ridges, more transverse pygidium, and broader, shallower pleural furrows. Examination of the type material of *N. taconica* and material from North Greenland referred to *Pagetides rjonsnitzkii* confirms that the two are not conspecific.

Parts of two collections (GGU 298553 & GGU 315112) from the section in southern Freuchen Land (Fig. 8A, locality 1; Fig. 10) were processed in acetic acid. The insoluble residues yielded over 100 immature specimens referable to *Pagetides elegans*. All were tightly enrolled. The mode of preservation of these specimens is unknown; unlike phosphatised material produced by this process from other samples, the material is not characteristically brown in colour (it is off-white) and has been etched by the acid used in the process (see Fig. 25.1a, b).

No record of enrolled specimens referred to the *Page-tides* has been found in the literature. The style of enrollment displayed by all the specimens can be described as sphaeroidal (Bergström 1973a, fig. 8c). Due to the severity of the etching the material is not further considered here.

During routine processing in acetic acid of samples from the Henson Gletscher Formation in Peary Land (Fig. 8A, locality 6; Fig. 11) a single collection (GGU 225714) produced rare specimens of cranidia, pygidia and thoracic segments. Due to its colour and lack of etching by the acetic acid this material is probably preserved in phosphate. It shows details of sculpture and convexity unlike that shown by larger specimens of the same species which may be due to more perfect preservation alone, or more probably, to real features of these immature growth stages (see Fig. 23). Specimens of the smallest phosphatic cranidia (which are about 700 microns in transverse width at the palpebral lobes; Fig. 23.3, 4) clearly demonstrate considerably greater elevation of the fixed cheeks in relation to the glabella and strongly tumid and exsagittally-elongated fixed cheeks, as opposed to the rather flat-topped cheeks described in the description

of the species. The facial sutures of the species are best shown in this small material, and the absence of ocular ridges even in these immature specimens is confirmed; the palebral lobes slope only moderately inwards. Most striking in the smallest specimens is the development of intricate sculpture; the cranidium has strong concentric ridges that contour the steeply rising cheeks and the glabellar spine. These ridges become fragmentary close to the anterior border furrow, grading into very coarse granules that continue onto the posterior of the anterior border. The outer part of the anterior border has low, continuous parallel ridges.

A larger immature cranidium (about 1400 microns transversely at palpebral lobe; Fig. 23.5) shows that the ridge-like sculpture has largely been replaced by closely-packed granules, with only some evidence of rather discontinuous ridges present on the outer part of the anterior border. Additionally, the anterior part of the glabella is relatively less depressed in relation to the fixed cheek as compared to the smallest specimens.

The same sample produced two types of thoracic segment which although of very similar size are markedly different. With different degrees of certainty, both are assigned to Pagetides elegans. Although not previously recorded in Pagetides, the development of different types of thoracic segments is known from species of Pagetia (see Jell 1975, p. 62, pl. 17, figs 7, 8). The first type of segment is characterised by the development of a very pronounced axial spine (see Fig. 23.2, 6) that is initially directed strongly upwards and is then curved strongly backwards. Axial furrows are not evident, the axis being defined by an abrupt change in exoskeletal slope. Interpleural furrows are indistinct adaxially, being narrow and deep distally. Pleurae are horizontal to the fulcral point, then very steeply downturned. At the fulcral point the posterior band is slightly swollen, being at a greater elevation than the adjacent area of the anterior band. Sculpture of the axial spine consists of contoured, interrupted ridges, whilst for the pleurae, weak ridges are in concentric arrangement around the posterior swelling at the point of geniculation. This type of segment is very probably correctly assigned to Pagetides elegans based on its close similarity to the unreleased segment of the transitory pygidium (Fig. 23.1).

The second type of thoracic segment (Fig. 23.8) assigned to this species lacks the axial spine and has a smooth axial ring. In all other aspects it is comparable to the previously described type of segment except that the sculpture on the outer part of the posterior pleural band is of low granules.

The similarities between the two forms promote tenuous assignment of both forms to *Pagetides elegans*. However, in the more than 100 complete and enrolled specimens of *Pagetides elegans* recovered from the samples previously described from Freuchen Land, only one type of thoracic segment is shown, namely, the type which lacks an axial spine. It is possible that two species are present, one in Freuchen Land and Lauge Koch

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Fig. 23. Pagetides elegans Rasetti, 1945. Henson Gletscher Formation. 1, meraspid pygidium with unreleased thoracic segment, dorsal view, MGUH 23190 from GGU collection 225714A, x 37. 2, 6, damaged thoracic segment, type 1, posterolateral and lateral views, MGUH 23177 from GGU collection 225714A, x 38. 3, damaged cranidium, dorsal view, MGUH 23170 from GGU collection 225714A, x 71. 4a, b, cranidium, anterolateral and lateral views, MGUH 23171 from GGU collection 225714A. a x 71, b x 88. 5, damaged cranidium, dorsal view, MGUH 23172 from GGU collection 225714A, x 36. 7a, b, pygidium, dorsal and lateral views, MGUH 23184 from GGU collection 225714A, x 37. 8, thoracic segment, type 2, posterolateral view, MGUH 23178 from GGU collection 225714A. x 37.

Land and another just a few kilometres east in Peary Land, but that it is only thoracic morphology that enables distinction. Alternatively, two forms may be represented, with variation reflecting temporal or spatial differences. In addition, since phosphatic material from the single Peary Land sample is disarticulated, it is possible that the two types of thoracic segment belong to different species.

Occurrence in North Greenland. – Henson Gletscher Formation, collection localities 1, 2 and 6 in Figs 8A, 10 and 11. Age: Early Cambrian, *Olenellus* Zone.

Pagetides rjonsnitzkii (Lermontova, 1940)

Fig. 24

- 1940 Pagetina rjonsnitzkii Lermontova, pl. 35, figs 7, 7a-b.
- 1951 Pagetina rjonsnitzkii Lerm.; Lermontova, p. 27, pl. 3, figs 7a-b.
- 1964 *Neopagetina rjonsnitzkii* (Lermontova); Lazarenko, p. 177, pl. 1, figs 22, 23, 25-27 (*non* 21, 24).

Type material. – Collected from bank of the River Gerbikan, Dzhagdi, eastern Siberia and of Early Cambrian age. The type collection (36/5156) is deposited in the Central Siberian Geological Museum, Novosibirsk, Russia.

Figured material. – Cranidium; MGUH 23191-23195 from GGU collection 218610. Pygidium; MGUH 23196-23202 from GGU collection 218610.

Other material. - GGU collection 218610 (abundant).

Diagnosis. – A species of *Pagetides* characterised by pygidial pleural fields transversed by five or six pairs of deep and narrow pleural furrows. Very narrow (tr.) pygidial axis of seven rings, prominent axial nodes on anterior six rings. Cranidium with S1 and S2 well developed, occasionally connected across glabella. Shallow preglabellar furrow.

Description. - Cranidium subsemicircular in outline. Moderately convex (tr.) glabella tapers gradually forwards from its widest point at the anterior of the occipital ring to S2, with the front of the glabella gently rounded. Basal width of glabellar variable between one-fifth and one-quarter posterior cephalic width. S1 positioned slightly forwards of glabellar midlength, formed of short, deep incisions directed slightly posteriorly and confluent with axial furrow. Occasionally connected by very shallow transglabellar furrow. S2 of similar morphology, more frequently connected across glabella by shallow furrow, and directed very gently backwards. Occipital furrow (SO) only impressed laterally, formed of deep, elongate pits, directed strongly posteriorly. From slightly behind S1, the posterior glabellar lobe and occipital ring are extended into a short, stout cranidial spine. Axial furrows broad (tr.) and shallow along length of L1, deepening forwards of S1 with rapid shallowing and narrowing around glabellar front. Preglabellar field moderately long (sag.), distinctly depressed, forming a marked pit in front of the glabella. Fixed cheeks highly convex (tr.), rising steeply from the posterior border and axial furrows, more gradually from the preglabellar field and anterior border furrow, and most steeply from the free cheek to become quite tumescent at about midlength, where at greatest elevation. Palpebral lobes short (exsag.), very gently arcuate, defined by narrow (tr.) furrow of moderate depth. Lobes centred at midpoint of L2, with exsagittal length approximately one-quarter sagittal glabellar length.

Transverse width of palpebral area about one and a quarter that of glabella across SO. Several specimens exhibit faint ocular ridges which are gently curved, and appear to terminate on the abaxial side of the axial furrow (Fig. 24.3). Anterior border wide (sag.), moderately convex and elevated above the border furrow. Border widest sagittally, narrowing to approximately half maximum width distally. Anterior border furrow broad (exsag.) and of moderate depth distally, shallowing slightly adaxially; occasionally indistinct around medial border expansion. Posterior border narrow (exsag.), expanding distally being widest at the fulcra. Border defined by narrow (exsag.), deep furrow which shallows adaxially and does not reach the axial furrow. Lateral border very narrow (tr.). Facial sutures not known with certainty.

Pygidium semicircular in outline, gently convex transversely and longitudinally. Articulating half-ring narrower (tr.), and lower than anteriormost axial ring from which it is separated by a well-impressed, straight or gently concave posteriorly, articulating furrow of constant depth. Axis tapers posteriorly and consists of seven prominent rings, and a short (sag.) terminal piece without spine or node. Axis does not reach posterior border, but is separated from it by a short (sag.) connective band. Anterior width of axis approximately one-fifth maximum pygidial width. Anterior six axial rings bear prominent axial nodes or spines that are broken at the base on all specimens; weakly developed node occasionally shown on seventh ring. The spine bases are not always central, but frequently are laterally displaced (Fig. 24.2). In lateral profile the bases indicate that the anterior three spines are directed vertically, whilst posteriorly the bases are directed moderately backwards, at least initially. Axis laterally defined by narrow (tr.) axial furrows of moderate depth, which shallow considerably posteriorly, and are continuous around the posterior of the axis. Anterior pleural strip of first pygidial segment widest (exsag.) at the fulcral points with long (tr.) articulating facets that are steep and flat, defined by gently curved furrow that attains its greatest width and depth at the fulcral points, and reaches to the inner edge of the lateral border. Pleural fields moderately to strongly convex (tr.), descending steeply to the border furrow, transversed by five or six pairs of deep and narrow pleural furrows which shallow slightly distally, and reach to the lateral border furrow. Three or four pairs of interpleural furrows apparent on some specimens; these are poorly impressed adaxially and very faint distally. The lateral border furrow is narrow (tr.), and of variable depth. Defines narrow (tr.) border of about constant width which is flat or gently convex, and along its posterior course is almost straight.

Sculpture has only been observed on the cranidial anterior border and consists of small pits which are mainly concentrated on the centre of the border (Fig. 24.3, 5).

Discussion. – *Pagetides rjonsitzkii* (Lermontova, 1940) has previously only been recorded from the Lower Cambrian of Siberia, and the North Greenland specimens



show some differences from the type series. Of particular note is the morphology of the occipital ring for, as described above, the specimens from Peary Land incorporate the posterior glabellar lobe and occipital ring into a cranidial spine. The cranidium figured by Lermontova (1940, pl. 35, fig. 7a) has a more distinct occipital ring, without an obvious spine. This led Jell (1975) to propose that a cranidial spine could not be cited in the diagnosis of Neopagetina. However, Lazarenko (1964, pl. 1, figs 21, 24, 25) figured three cranidia that were assigned to N. rjonsnitzkii and, although two of these are excluded from the species, the remaining cranidium (fig. 25) exhibits the preoccipital lobe and occipital ring being extended back into a cranidial spine. The two excluded cranidia have very well developed ocular ridges, and an occipital ring that is clearly defined and bears a small median node. These specimens are conspecific with those figured as Neopagetina pararjonsnitskii Egorova & Shabanov, 1972 in Savitsky et al. (1972). This species is discussed later.

Occurrence in North Greenland. – Henson Gletscher Formation, collection locality 5 in Fig. 8A. Age: Early Cambrian, *Olenellus* Zone.

Remarks on other species of 'Neopagetina'. - 'Neopagetina' shishkini Egorova, 1972 (see also Egorova et al. 1976) is here not referred to Pagetides for the characteristics of both cranidium and pygidium are inconsistent with such an assignment. The pygidium resembles Pagetia with an axis that overhangs the posterior border furrow, and terminal segment that is swollen and has a broken spine base. The cranidium has an unusual morphology with the glabella divided into two distinct lobes by a transverse furrow at about two-thirds length from the posterior margin. In lateral profile the posterior lobe is greatly elevated above the anterior (see Egorova 1972, pl. 1, figs 1b, 2b). The occipital furrow is deep and continuous across the axial line, and the occipital ring is extended backwards into a long, stout spine. In all these features the specimens differ from Pagetides.

'Neopagetina' nomokonovi Semashko, 1969 was described as part of a Middle Cambrian fauna from the Batenevsky Mountain Range, Siberia; two cranidia and a pygidium were illustrated. It seems that the two exoskeletal parts do not belong in the same family, and that neither of them is correctly assigned to *Pagetides*. The cranidia have a gently tapered glabella, a well-defined occipital ring without spine or node and a very short (sag.), deep preglabellar field; additionally the anterior border is narrow (sag.) and the anterior margin almost straight in front of the glabella. This combination of characters is more typical of *Calodiscus*. The illustrated pygidium is that of an oryctocephalid, not an eodiscid, and is comparable to specimens herein described as *Ovatoryctocara*? sp. A, from the Henson Gletscher Formation, to which taxon it is assigned.

Wrong association of exoskeletal elements is also suspected in another species originally referred to Neopagetina, namely 'N'. dzhagdinica Repina, 1975. The cranidia of this species are poorly figured (Repina 1975, pl. 39, figs 1-10), but the characteristics are a short (sag.), parallel-sided glabella with strongly rounded anterior, welldefined occipital ring without spine or node, very long (sag.) preglabellar field, wide (tr.) palpebral areas and a narrow cranidial border. The morphology is not compatible with an eodiscoid assignment and the referred pygidia are representatives of a dorypygid. The posteriorly-tapering axis consists of six rings and a terminal piece, with at least the anterior five bearing axial nodes on the posterior margin. Pleural fields are traversed by four or five pairs of deep pleural furrows that reach to the border furrow, and the pygidial border is flat with several pairs of short border spines. The possession of pygidial border spines is in contradiction to the description of this species given by Repina (1975) which states that the lateral margin is smooth. The figured pygidia have all the characteristics of Kootenia Walcott, 1889. Importantly Repina (1975) described a new species, Kootenia khabarovica, as part of the same fauna. It seems most probable that the pygidia assigned to 'N'. dzhaginica in fact belong to that species of Kootenia.

Repina (in Okuneva & Repina 1973) described 'N'. *pusilla* from very poorly-preserved Russian material which hardly supports diagnosis of a species. Several forms may be represented but there is no evidence that any of them is *Pagetides*.

'*Neopagetina' pararjonsnitskii* Egorova & Schabanov in Savitsky *et al.* 1972 may belong to a new unnamed genus since the occipital ring is defined by a continuous furrow, bears only a small median spine and the ocular ridges are wide (exsag.), with high relief. The associated pygidium has a wide, flat border, with an axis formed of only five rings.

Fig. 24. *Pagetides rjonsnitzkii* (Lermontova, 1940). Henson Gletscher Formation. 1, cranidium, partially exfoliated, dorsal view, MGUH 23195, x 19. 2, pygidium, partially exfoliated, dorsal view, MGUH 23197, x 18. 3, cranidium, partially exfoliated, dorsal view, MGUH 23191, x 16. 4, pygidium, partially exfoliated, dorsal view, MGUH 23201, x 14. 5, cranidium, partially exfoliated, dorsal view, MGUH 23193, x 18. 6, pygidium, partially exfoliated, dorsal view, MGUH 23202, x 20. 7, pygidium, partially exfoliated, dorsal view, MGUH 23198, x 17. 8, pygidium, partially exfoliated, dorsal view, MGUH 23199, x 13. 9, cranidium, partially exfoliated, dorsal view, MGUH 23199, x 13. 9, cranidium, partially exfoliated, dorsal view, MGUH 23194, x 15.5. 11, pygidium, partially exfoliated, dorsal view, MGUH 23194, x 15.5. 11, pygidium, partially exfoliated, dorsal view, MGUH 23194, x 15.5. 11, pygidium, partially exfoliated, dorsal view, MGUH 23196, x 16. All from GGU collection 218610.

Family Weymouthiidae Kobayashi, 1943

Diagnosis. – After Jell (1975: 27). Blind eodiscoids with fixed cheeks confluent anteriorly, or glabella reaching border furrow. Genal angle spinose or rounded. Bacculae absent. If present, spines on the cephalic axis clearly glabellar or occipital. Pygidial axis usually wider (tr.) than pleura plus border; usually more than seven axial rings or transaxial furrows effaced. Axis usually slightly raised above pleural areas. Pleural furrows generally absent. Thorax of three segments where known.

Discussion. – The Eodiscidae was erected by Raymond (1913) to include all eodiscids previously assigned to *Microdiscus* Salter, 1864, for this genus was shown to be invalid by Raymond (1913). Subsequent workers either followed this classification (e.g. Richter & Richter 1941) or produced complex classifications, said to be phylogenetic, with many families and subfamilies (e.g. Kobayashi 1943). More recently, two families have been accepted; the Eodiscidae and the Pagetiidae Kobayashi, 1935, with Rasetti (1952) considering Pagetiidae to include sutured and oculate Agnostida, and the Eodiscidae to be sutureless forms. As discussed by Jell (1975: 14), this classification now appears invalid, for these features may not be as phylogenetically significant as was previously believed.

Jell (1975) analysed forty morphological characters of the 34 eodiscid genera that were known to him at the time and recognised two families, the Weymouthiidae Kobayashi, 1943 and Eodiscidae Raymond, 1913. His numerical analysis showed there to be no single character that can be used to distinguish the families, a concept which had been the basis of previous classifications. Öpik (1975) also reviewed eodiscid classification and revived the Weymouthiidae. The revised classification of Öpik differs from that of Jell (1975) in that a third family, the Calodiscidae Kobayashi, 1943, is also recognised. Additionally only 22 genera were considered to be valid members of the suborder Eodiscina, as opposed to the 34 recognised by Jell (1975). Öpik (1975) did not explain the reasons behind his classification and in particular the grouping of Calodiscus, Neocobboldia and Stigmadiscus into the Calodiscidae. This classification is not accepted due to the lack of discussion of its basis, and that of Jell (1975) is followed here.

The classification of Zhang *et al.* (1980: 420) is only based on "... the presence or absence of facial sutures, eye or eye tubercles". This scheme is not considered to be viable, for as pointed out by both Jell (1975: 14) and Öpik (1975: 19), the presence or absence of eyes and facial sutures are not diagnostic at that high taxonomic level.

As noted above, Babcock (1994a) recently suggested that eodiscid trilobites may be polyphyletically derived from polymeroids, but did not present a classification of eodiscid trilobites. Synonym. – Paradiscus Kobayashi, 1943 (after Rasetti 1952).

Type species. – By original designation; *Eodiscus* (*Serrodiscus*) serratus Richter & Richter, 1941, from the Early Cambrian serratus-band in the Herrerias-Mergel, near Cala, southern Spain.

Diagnosis. – After Rushton (1966: 11). Cephalon semielliptical. Glabella long, simple, conical or approximately parallel-sided, sharply rounded in front, with weak glabellar furrows or unfurrowed. Genae confluent anteriorly or separated by short (sag.) preglabellar furrow. Border convex, with up to eight pairs of tubercles. Pygidial axis divided into more than eight rings, transversely wider than the unfurrowed pleural field. Border narrows posteriorly, bearing ventral spines.

Remarks. - Serrodiscus has previously been recorded from North Greenland by Dawes (1976: 277), and more recently by Peel (1979: 116) who referred a small collection from northern Nyeboe Land to S. bellimarginatus (Shaler & Foerste, 1888). As noted by Dawes & Peel (1984), this material is here considered to belong to the closely related S. speciosus (Ford, 1873). Further collections from the Aftenstjernesø Formation in northern Nyeboe Land contain specimens referred to S. speciosus, S. daedalus Öpik, 1975 and S. latus? Rasetti, 1966a. This material has been deformed to varying degrees, and the descriptions have been based on the least deformed specimens. Palmer & Peel (1979) reported Serrodiscus from the lower part of the upper mudstone-dominated unit of the Buen Formation in southern Peary Land (Fig. 3, locality 1) in association with Olenellus hyperboreus and Limniphacos perspicullum; this fragmentary material is not described here, although Serrodiscus sp. A is described from the uppermost Buen Formation in eastern Peary Land where it is associated with Olenellus svalbardensis (Fig. 3, locality 3).

Serrodiscus daedalus Öpik, 1975

Fig. 25.3, 9-11

1973 Serrodiscus aff. agnostoides Poletaeva, 1960; Okuneva & Repina, p. 156, pl. 29, fig. 7.

1975 Serrodiscus daedalus sp. nov. Öpik, p. 27, pl. 3, figs 5-9.

Fig. 25. Lower Cambrian trilobites.

1a, b. Pagetides elegans Rasetti, 1945. Henson Gletscher Formation. Complete, enrolled specimen, dorsal and anterior views of thorax and pygidium, MGUH 23189 from GGU collection 298553A, x 39.

2. Serrodiscus latus? Rasetti, 1966. Aftenstjernesø Formation. Damaged cephalon, dorsal view, MGUH 23596 from GGU collection 319744, x 4.3.

3, 9-11. Serrodiscus daedalus Öpik, 1975. Aftenstjernesø Formation. 3a, b, cephalon, partially exfoliated, dorsal and lateral views, MGUH 23206 from GGU collection 319763, x 6.4. 9a, b, cephalon, internal mould, dorsal and lateral views, MGUH 23204 from GGU collection 319742, x 4.3. 10, cephalon, internal mould, dorsal view, MGUH 23203 from GGU collection 319742, x 5. 11, cephalon, latex of external mould, dorsal view, MGUH 23205 from GGU collection 319742, x 4.3.

4, 5, 7. *Peronopsis roddyi* (Resser & Howell, 1938). Henson Gletscher Formation. 4, complete specimen, internal mould, dorsal view, MGUH 23281 from GGU collection 298545, x 17.8. 5, cephalon, internal mould, dorsal view, MGUH 23135 from GGU collection 298545, x 13.5. 7, complete specimen, internal mould, dorsal view, MGUH 23282 from GGU collection 298545, x 17.

6, 8. *Serrodiscus* sp. A. Buen Formation, GGU collection 256959. 6, cephalon and thoracic segment, internal mould, dorsal view, MGUH 23216, x 2.8. 8, cephalon (MGUH 23217) and pygidium (MGUH 23218), partially exfoliated, dorsal view, x 2.1.

1b 5 1a 7 3a 3h 9a 10 9b

Type material. – Holotype cephalon CPC 13167 from the Lower Cambrian Cymbric Vale Formation of New South Wales, Australia. The type series is housed in the Bureau of Mineral Resources, Geology and Geophysics, Canberra, Australia. Figured material. – Cephalon; MGUH 23203-23205 from GGU collection 319742, MGUH 23206 from GGU collection 319763.

Other material. – GGU collections 319742, 319762 and 319769.

Remarks. – The diagnosis of Öpik (1975: 27) is very brief and includes several characteristics which are not diagnostic, such as "well impressed furrows including a transcurrent glabellar furrow and distinguished by its very wide cephalic, and pygidial rim". The type series falls within the range of morphology exhibited by the material from North Greenland; due to the better preservation of the latter, the diagnosis has been emended.

Emended diagnosis. – A species of *Serrodiscus* with tapered glabella marked by three pairs of glabellar furrows. S1 and S2 short, deep incisions, directed backwards and occasionally connected across glabella by shallow furrow. S3 more distinctly continuous across glabella, concave backwards with slight shallowing over sagittal line on some specimens. L1 and occipital ring combined to form stout spine directed upwards and backwards. SO represented distally by isolated pits.

Description. - Cephalon gently convex (tr. & sag.). Glabella tapers forward with strongly rounded anterior; preglabellar field very short (sag.). For some specimens there is more or less even reduction in width along the glabella, whilst for others there is rapid taper until the level of S2, then more gently tapered forward of S2, producing a concave outline. Axial furrow very wide and deep; preglabellar furrow shallower and narrower. Three pairs of well-developed glabellar furrows, with all pairs reaching axial furrow; S1 defined adaxially by short (tr.), deep, slot-like incisions, with the furrow being very shallow or absent over the axial line, when present distinctly convex anteriorly. S2 of moderate length and depth, directed gently backwards, and occasionally connected across glabella by shallow furrow. S3 positioned at approximately glabellar midlength and more distinctly continuous across glabella, being moderately concave posteriorly. L2 and L3 strongly bulbous in appearance. SO represented distally by very short, deep pits that are directed backwards at higher angle than S1. SO not continuous across glabella and isolated from axial furrow. Occipital ring and L1 incorporate a stout spine of moderate length that is upturned, and elevated above all other parts of the cephalon. Gena gently to moderately convex (tr.) and as wide as glabella at level of S3. Border furrow broad and of moderate depth in front of glabella, narrowing posterolaterally. Border very wide (sag.) and gently convex, narrowing to less than half its maximum width posterolaterally. Border with 18 or 19 large tubercles along entire length with tubercle size decreasing posteriorly. Posterior border furrow wide and deep, curved gently anterolaterally and continuous with lateral border furrow. Posterior border short, with transverse width less than basal glabellar width, subtriangular in outline with distal fulcrum.

Discussion. – Some variation exists within the type series, in particular the width of the cephalic border. Though both populations are small (7 cephala in the type series and 8 from North Greenland), in the type material the cephalic border is consistently of greater relative sagittal length. Such variation is not considered sufficient to place the North Greenland material in a separate species. The better preservation of the material from North Greenland has enabled a more detailed description of glabellar lobation; in particular it is now known that in addition to S3, both S2 and S1 may be continuous across the glabella. It has also been determined from the new material that there is a pronounced occipital spine that incorporates both L1 and the occipital ring.

Öpik (1975: 27) compared S. daedalus with S. fossuliferus Repina in Repina et al. 1964 from the Altai Sayan Mountain region of Siberia, distinguishing the Siberian form by its narrower cephalic border. The width of this border does not serve to separate the two species, though S. fossuliferus can be separated by fewer tubercles on the cephalic border, with these being almost obsolete anteriorly; in addition, the preglabellar field is longer (sag.) and the occipital ring does not extend into an upturned spine. The genae of S. fossuliferus are also considerably wider (tr.) than the glabella at the level of S2, justifying separation of the two species. Öpik (1975: 27) also compared S. daedalus with S. Ilarenai (Richter & Richter, 1941) from Spain, distinguishing the latter on a short (sag.), unfurrowed glabella and short (sag.) pygidial axis. S. Ilarenai differs considerably from S. daedalus, for the border has only 5 or 6 pairs of weakly developed tubercles which become obsolete anteriorly, the glabella has a faint median node at the posterior, and the occipital ring is simple, without a spine, and is defined by a continuous furrow. It is possible that the glabella is not unfurrowed on all specimens of S. Ilarenai as stated by Öpik, for Rushton (1966: 24) described "... three faint paired impressions" on the glabella, although he did concede that these may be adventitious.

Occurrence in North Greenland. – Aftenstjernesø Formation, collection localities 2 and 3 in Figs 4 and 5. Age: Early Cambrian, *Olenellus* Zone.

Serrodiscus latus? Rasetti, 1966a

Fig. 25.2

1966a Serrodiscus latus Rasetti, new species, p. 34, pl. 10, figs 12-15.

1967 Serrodiscus latus Rasetti; Rasetti, p. 51, pl. 14, figs 9-12.

Type material. – From Lower Cambrian strata of the Taconic sequence, New York State, U. S. A. Holotype cephalon, USNM 146024 in the collections of the Natural History Museum, Smithsonian Institution, Washington D. C.

Figured material. – Cephalon; MGUH 23596 from GGU collection 319744.

Fig. 26. Trilobites from the Aftenstjernesø Formation.

1-8, 10. Serrodiscus speciosus (Ford, 1873). 1, cephalon, partially exfoliated, dorsal view, MGUH 23208 from GGU collection 319742, x 3.5. 2, damaged cephalon, dorsal view, MGUH 23209 from GGU collection 319764, x 4.2. 3, complete specimen, latex of external mould, dorsal view, MGUH 23215 from GGU collection 319762, x 2.8. 4a-c, pygidium, internal mould, dorsal, posterior and lateral views, MGUH 23211 from GGU collection 319742, x 4.9. 5, pygidium, latex of external mould, dorsal view, MGUH 23214 from GGU collection 319742, x 6. 6, pygidium, latex of external mould, dorsal view, MGUH 23213 from GGU collection 319742, x 3.5. 7, cephalon, partially exfoliated, dorsal view, MGUH 23207 from GGU collection 319742, x 4.2. 8a, b, pygidium, partially exfoliated, dorsal and lateral views, MGUH 23210 from GGU collection 319742, x 5.2. 10, pygidium, partially exfoliated, dorsal view, MGUH 23212 from GGU collection 319742, x 4.2.

9, 11. Olenellus sp. B. 9, cephalon and partial thorax, latex of external mould, dorsal view, MGUH 23288 from GGU collection 319742, x 1.4. 11, cephalon, dorsal view, MGUH 23289 from GGU collection 319757, x 2.8.



Remarks. – Associated with the specimens of *Serrodiscus speciosus* and *S. daedalus* is a single cephalon which may belong to *S. latus*. This specimen shares with the type material of *S. latus* a very poorly defined occipital ring, SO is only defined laterally by short, shallow fur-

rows. A tapered glabella extends almost to the border furrow that is defined by deep axial furrows, and the cephalic border attains maximum width sagittally. Differences are that the lateral border of *S. latus* has a few pairs of low nodes posteriorly, and on the posterior bor-

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der the fulcrum bears short, posteriorly directed spines. The absence of nodes on the border is probably not a specific character (as discussed), but as both fulcra are damaged on the single specimen to hand, the cephalon is referred to *S. latus* with some doubt. As discussed by Rasetti (1966a: 34), in the absence of a pygidium it is questionable if the type material should not be referred to *Calodiscus* or *Cobboldites*. Rasetti (1967: 51), however, tentatively assigned two pygidia to the cephala which, if the association is correct, confirm an assignment to *Serrodiscus*; in the absence of more material this classification is maintained.

Occurrence in North Greenland. – Aftenstjernesø Formation, collection locality 3 (Figs 4 and 5). Age: Early Cambrian, *Olenellus* Zone.

Serrodiscus speciosus (Ford, 1873)

Fig. 26.1-8, 10

- 1873 Microdiscus speciosus Ford, p. 137, figs 2a-b.
- 1952 Serrodiscus speciosus (Ford); Rasetti, p. 444, pl. 52, figs 1-11 (includes complete synonomy).
- 1956 Serrodiscus speciosus (Ford); Lochman, p. 1381, pl. 5, figs 13-21.
- 1964 Serrodiscus speciosus (Ford); Theokritoff, p. 185, pl. 2, figs 1-8.
- 1964 Serrodiscus levis Repina in Repina et al., p. 261, pl. 38, figs 15, 16.
- 1967 Serrodiscus speciosus (Ford); Rasetti, p. 50, pl. 3, fig. 29.
- 1978 Serrodiscus levis Repina; Repina & Romanenko, p. 14, pl. 1, figs 11, 13,16.
- 1979 Serrodiscus bellimarginatus (Shaler & Foerste, 1888); Peel, p. 116, fig. 2 (= S. speciosus, Dawes & Peel 1984).
- 1981 Serrodiscus speciosus (Ford); Gil Cid, p. 30, pl. 1, figs 4-6, pl. 2, figs 1, 2, 6-9.

Type material. – From the Lower Cambrian Schodack (= West Castleton) Formation. The type locality is on the ridge in the eastern suburb of the city of Troy, New York State (Rasetti 1952: 445). The repository of the type series is New York State Museum, Albany, New York, U.S.A.

Figured material. – Cephalon; MGUH 23207-23208 from GGU collection 319742, MGUH 23209 from GGU collection 319764. Pygidium; MGUH 23210-23214 from GGU collection 319742. Complete specimen; MGUH 23215 from GGU collection 319762.

Other material. - GGU collections 319742, 319755, 319759-319761, 319764, 319765.

Diagnosis. – A species of *Serrodiscus* with tapered glabella, no occipital spine or node, a pygidium with well-defined axial segmentation of nine or ten rings, with axial nodes on up to the seventh ring.

Description. - Cephalon moderately convex (tr. & sag.) with length:width ratio 7:8. Glabella moderately convex transversely; in lateral profile horizontal over posterior four-fifths, sloping rapidly downward over anterior fifth to the preglabellar furrow. Glabella tapers moderately forward over posterior two-fifths, then more gradually anteriorly, producing a slightly concave outline; anterior strongly rounded. Preglabellar field slopes down to border furrow. Sagittal length of preglabellar field onetwelfth glabellar length. Three pairs of glabellar furrows, barely apparent on some specimens, and absent on others. When present furrows represented by diffuse shallow areas. All furrows reach axial furrow, but not sagittal line. Axial furrow broad (tr.) and deep. Occipital furrow indistinct, represented laterally by broad and shallow furrow, not crossing axial line. Short (sag.) occipital ring wider than glabella across L1, posterior margin gently curved. Gena as wide (tr.), or slightly wider than, glabella at midlength. Border furrow wide (sag.), narrowing posteriorly, and moderately deep throughout. Border gently convex, narrowest posterolaterally with increase in width anteriorly, attaining maximum width in front of glabella. Border with ten pairs of nodes whose prominence decreases anteriorly. Posterior border furrow with gradual increase in width (exsag.) and depth distally, confluent with lateral furrow. Posterior border very narrow axially, widening distally to prominent fulcrum.

Thorax of three segments known from only one poorly preserved specimen which is inadequate for description.

Pygidium subtriangular in outline, moderately convex (tr. & sag.). Axis tapers posteriorly and extends almost to the posterior border furrow. Sagittal length of connective band very short, being at most one-twentieth sagittal pygidial length. Anteriorly axis occupies over one-half transverse pygidial width which is distance between prominent fulcra. Axis forms about one-quarter of the pygidial width where this is at its greatest. In lateral profile axis slopes strongly downwards behind the third axial ring. Over the anterior three rings axis is on average horizontal. Axial furrow anteriorly broad (tr.) and deep, narrowing posteriorly, and continuous around the posterior of the axis where it is very narrow (sag.). For large specimens furrow indistinct around posterior of axis. Axis formed of nine or ten rings and a terminal piece. Axial rings moderately convex (tr.), the anterior four rings with prominent median nodes. Articulating half-ring defined by wide (sag.), deep furrow. Pleural fields unfurrowed and slope strongly outwards to the border furrow over distal two-thirds, adaxial third horizontal. Border furrow wide and deep, being widest at about half length, narrowing anteriorly and posteriorly. Border narrower than furrow, gently convex, narrowing posteriorly, and bearing eight pairs of short border spines which point ventrally, and are approximately equally spaced along the entire border.

Discussion. – Due to deformation this material shows a wide range of variation in glabellar furrow morphology with more intensely deformed specimens not preserving furrowing. Similarly, axial furrow morphology is diverse with much narrower furrows in flattened specimens (compare Fig. 26.1 and 7).

The form morphologically closest to Serrodiscus speciosus is S. bellimarginatus (Shaler & Foerste, 1888); in fact they are not easily separated. In the opinion of Rasetti (1952: 446), S. bellimarginatus differs in a less tapered glabella, development of an occipital spine, more conspicuous genal spines, nodes on all axial rings and stronger pygidial border spines. In discussion of S. speciosus, Rasetti (1952) noted exceedingly short and slender genal spines. These spines have not been observed following study of the figured material, and other unfigured specimens. Indeed neither S. speciosus nor S. bellimarginatus has genal spines and Rasetti (1952) appears to have misinterpreted a more prominent fulcrum on specimens of S. bellimarginatus as a genal spine. Specimens of S. bellimarginatus from the Purley Shales, Warwickshire, England described and figured by Rushton (1966, p. 13, pl. 1, figs 2-5), agree with the distinctions of the two species proposed by Rasetti (1952).

The material from North Greenland occupies somewhat of an intermediate position between *S. speciosus* and *S. bellimarginatus* for the pygidia have axial nodes on at most the anterior four rings, and the pygidial border spines are of equal development to those on specimens of *S. bellimarginatus*. However, in the tapered glabella and occipital ring without a spine, the material is closer to *S. speciosus*, and it is to this species that assignment is made.

Serrodiscus speciosus appears to be a very variable species, for from an examination of the material assigned to *S. speciosus* by Lochman (1956), there may be axial nodes on up to the anterior seven rings, and a sculpture of low granules on the pleural fields is not uncommon.

Similarities also exist with S. mackenziensis Fritz, 1973, which Fritz (1973) separated from S. bellimarginatus by its tapered glabella and lack of a node or spine on the occipital ring. No comparisons were made with S. speciosus with which it has much in common. S. mackenziensis can be distinguished from S. speciosus by a pygidium that has relatively narrower (tr.) pleural fields, and hence a more elliptical outline, an axis consistently formed of ten rings, all with an axial node, and a pygidial border with seven pairs of spines that are directed ventrally and are evenly spaced along the border. Additionally, all parts of the cephalon and pygidium have a sculpture of raised reticulate ridges. Differences between the two species in the number of cephalic border nodes appear not to be of specific value, for Rasetti (1952: 446) noted considerable variation in specimens of S. speciosus from the Taconic sequence of New York State.

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Repina (in Repina *et al.* 1964) described *Serrodiscus levis* from Lower Cambrian strata of the Altai Mountains, Siberia. The two figured cephala are comparable in morphology to the material from northern Nyeboe Land of *S. speciosus*, and are here regarded as being conspecific. An additional cephalon figured as *S. levis* by Repina & Romanenko (1978) from the Altai Mountains is also included within *S. speciosus*.

Serrodiscus murtucus was described by Repina (1979a) from the Mana Trough, eastern Sayan, Siberia, on the basis of three cephala (two of which are damaged) and the species was compared to both S. subclavatus Rasetti, 1966a from the Early Cambrian Taconic sequence of New York State, U. S. A. and S. bellimarginatus. Repina distinguished S. murtucus from the latter by a shorter (sag.) preglabellar field and nodes that are less clearly developed on the cephalic border. The presence of a preglabellar field was used to distinguish S. murtucus from S. subclavatus. The illustrated cephalon of S. murtucus differs from S. subclavatus in glabellar outline since it does not taper strongly anteriorly and reach to the cephalic border; it also differs in the lack of pronounced fulcral spines. It is most similar to S. bellimarginatus and S. speciosus but, in the absence of a pygidium, it is difficult to ascertain to which species the material should be assigned. In possessing a glabella that does not taper anteriorly it is closer to S. bellimarginatus, and furthermore, there appears to be a small spine on the occipital ring. S. murtucus is therefore best placed in synonymy with S. bellimarginatus.

Occurrence in North Greenland. – Aftenstjernesø Formation, collection localities 2 and 3 (see Fig. 10). Age: Early Cambrian, *Olenellus* Zone.

Serrodiscus sp. A

Fig. 25.6, 8

Figured material. – Cephalon; MGUH 23216-23217 from GGU collection 256959. Pygidium; MGUH 23218 from GGU 256959.

Remarks. – Associated with specimens of *Olenellus svalbardensis* Kielan, 1960 from the uppermost Buen Formation in eastern Peary Land (Fig. 3, locality 3) are two cephala and one pygidium which are tentatively recognised as *Serrodiscus* sp. A. These specimens are distinguished from *S. speciosus* by the cephalic border furrow which is very wide (sag.) and shallow in front of the glabella. Also the border is almost flat without nodes although, as noted previously, the morphology of the nodes is highly variable within a species. The pygidium differs in that the axis is formed of eleven rings (rather than 9 or 10), and the flat border bears ten or eleven (rather than 8) pairs of short, stout spines.

Occurrence in North Greenland. – Buen Formation, collection locality 3 in Fig. 3. Age: Early Cambrian, *Olenellus* Zone.

Order Redlichiida Richter, 1933 Suborder Olenellina Walcott, 1890

Remarks. - In the past quarter of a century several revisions of olenelline classification have been made and these are summarised conveniently by Palmer & Repina (1993, table 1). Bergström (1973b) recognised three families (Olenellidae Walcott, 1890, Holmiidae Hupé, 1953 and Daguinaspididae Hupé, 1953). Subsequently, Repina (1979b) took account of the order of appearance of cephalic features during the Early Cambrian in deriving a phylogeny of olenellids, and split the Daguinaspididae (sensu Bergström 1973b) into 4 families: Archaeaspididae Repina, 1979b, Daguinaspididae, Fallotaspididae Hupé, 1953 and Nevadiidae Hupé, 1953, transferring the subfamily Callaviinae to the Holmidae. In addition, she transferred Wanneria Walcott, 1910 from the Holmiidae (sensu Bergström 1973b) to the Olenellidae as a subfamily Wanneriinae. Ahlberg et al. (1986) accepted much of Repina's (1979b) classification in recognising 6 families: Olenellidae, Wanneridae Hupé, 1953, Holmiidae, Callaviidae Poulsen in Moore 1959, Daguinaspididae and Nevadiidae.

Palmer & Repina (1993) recognised 2 superfamilies (Olenelloidea and Fallotaspidoidea) containing 2 families (Olenellidae and Holmiidae) and 5 families (Fallotaspididae, Archaeaspididae, Judomiidae Repina, 1979b, Neltneriidae Hupé, 1953 and Nevadiidae) respectively. A feature of this classification, which accommodates almost 50 genera, is the establishment of 8 subfamilies distributed between 2 families within the Olenelloidea; only 2 subfamilies are recognised within the 5 families of the Superfamily Fallotaspidoidea. By comparison, to illustrate the general trend in the development of the classifications, Bergström (1973b) established no subfamilies within the Olenellidae and Holmiidae of his usage and recognised most of the fallotaspidoidean families of Palmer & Repina (1993) at the level of subfamily.

The supra-generic classification employed here follows Palmer & Repina (1993).

Superfamily Fallotaspidoidea Hupé, 1953 Family Nevadiidae Hupé, 1953 Genus *Buenellus* Blaker, 1988

Type species. – By original designation; *Buenellus higginsi* sp. nov. Blaker, 1988, p. 36, figs 3-6.

Remarks. – Conway Morris *et al.* (1987) reported a spectacular new fauna of mainly weakly skeletised metazoans of Burgess Shale-type from deeper water, outer-shelf mudstones from the Lower Cambrian of North Greenland. The new fauna was collected from the lower part of the Buen Formation (not from the upper part as originally supposed, cf. Conway Morris & Peel 1990) from a single locality in Sirius Passet, adjacent to J. P. Koch Fjord, western Peary Land (Fig. 3, locality 5). Descriptions of some of the rich fauna were published by Conway Morris & Peel (1990, 1995). Rigby (1986) and Budd (1993, 1995). A prominent member of the Sirius Passet fauna is the nevadiid trilobite *Buenellus* Blaker, 1988, named after the formation of origin.

Diagnosis. – Nevadiid with elongate glabella tapering gently forward, not reaching border. Wide (sag.) occipital ring. Palpebral lobes of moderate length (exsag.), narrow (tr.); widening as glabella is approached anteriorly. Wirelike intergenal and metagenal ridges meet at posterior border at position of intergenal spine. Short, stout genal spines, not advanced. The border and border furrow are weakly defined anteriorly and anterolaterally. Thorax and pygidium of 19 segments of which the pygidium usually forms only the posteriormost segment. Thorax tapers rapidly backwards posteriorly of the eighth segment. Pleurae sigmoidally curved with short deep furrow. Axial rings with medial node. Pygidium formed of a single segmental plate.

Discussion. – Palmer & Repina (1993) assigned *Buenellus* to the Family Nevadiidae Hupé, 1953. The material from the Buen Formation resembles *Nevadella* Raw, 1936 from the Lower Cambrian of North America, but that genus has much longer (exsag.) and wider (tr.) ocular lobes that extend back to the level of the occipital ring, and has genal spines that extend back beyond this level. In addition, *Nevadella* lacks the intergenal and metagenal ridges, as well as intergenal spines. The thorax of *Nevadella* is known to have from 18 to 23 segments; it lacks macropleural segments, and the pygidium is small. In these features *Buenellus* is similar to *Nevadella*.

Nevadia Walcott, 1910 from the Lower Cambrian of North America and the northern Siberian platform (Palmer & Repina 1993: 31) has very wide (tr.) extraocular cheeks, a strongly furrowed glabella and lacks metagenal ridges. The ocular lobes are of similar length but are much wider (tr.) than in *Buenellus*, with intergenal ridges extending from their posterior tip. The thorax is considerably different from that of *Buenellus* having 28 segments, with the pleurae extending into long curved spines. The pygidia, however, are similar.

Whittington (1989: 125) commented that the diagnosis of *Buenellus* includes characters observed in species of *Nevadia*, and that the significance of supposedly distinctive characters in *Buenellus* is uncertain. He considered *Buenellus higginsi* Blaker, 1988 to be an example of the taxonomic problems posed by olenellids at the generic level. The development of an intergenal spine and ridge are characteristic of species assigned to *Callavia* Matthew, 1897 from North America. For *Callavia* species, however, the position of this spine is different from that in *Buenellus*, being very close to the genal angle, and no metagenal ridge is developed. Additionally, the ocular lobes are more strongly crescentic, and of greater relative length in *Callavia*. In the type species, *C. broeggeri* (Walcott, 1890), the occipital ring bears a long, backwardly-directed, slender spine. The glabella has four or five well-developed pairs of furrows in all species assigned to *Callavia*. The thorax and pygidium are similar to those of *Buenellus* with up to 18 segments in the thorax, each with short, stout, posterolaterally-directed spines, a pleural furrow that extends over the adaxial half of the pleura and axial rings with a short median node. The pygidium is formed of a single plate with a short median spine on the posterior margin.

Buenellus shows some similarities to Holmia Matthew, 1890 which is known from the Lower Cambrian of Europe, North America and the Siberian platform (Palmer & Repina 1993: 26) in that for both genera the cephalic border is poorly defined in front of the glabella, and metagenal and intergenal ridges are present. In general, like Buenellus, species of Holmia do not have a macropleural thoracic segment, and the distance from the axis to the pleural fulcrum is short. The glabella in *Holmia*, however, is strongly furrowed, and the expanded anterior lobe extends to the anterior border. The palpebral lobes of *Holmia* species are considerably wider (tr.), and often marked by an epipalpebral furrow. In the type species, *H. kjerulfi* (Linnarsson, 1871), the thorax is formed of 16 segments which taper regularly backwards, and have well-developed axial spines posterior to the tenth segment. The pygidium of *Holmia* is unlike that of *Buenellus*, being formed of at least two segments and a terminal piece in the axis.

Both intergenal and metagenal ridges are developed in species of *Kjerulfia* Kiær, 1917, known from the Lower Cambrian of Norway; these converge on the posterior border at the position of an intergenal spine or node. The taxonomic importance of intergenal and metagenal ridges is uncertain for they are present in genera assigned to different superfamilies, for example *Fallotaspis* Hupé, 1953 and *Kjerulfia*. *Kjerulfia* differs from *Buenellus* in having much wider (tr.) ocular lobes, and a strongly-furrowed glabella. In addition, the cephalic border is wider. The thorax of *Kjerulfia* has up to 17 segments with distinct medial axial nodes that increase in length posteriorly



Fig. 27. *Buenellus higginsi* Blaker, 1988. Buen Formation. 1, paratype, damaged complete specimen, dorsal view, MGUH 17.586 from GGU 319571, x 2.5. 2, paratype, damaged complete specimen, dorsal view, MGUH 17.589 from GGU collection 319571, x 2.

from the twelfth segment, with the posterior two axial rings possessing long, slender spines. The pygidium is comparable in form to *Buenellus*.

In spite of the reservations of Whittington (1989), *Bue-nellus* is maintained as a separate genus. Palmer & Repina (1993) accepted this status, placing it together with *Nevadia*, *Nevadella*, *Pseudojudomia* Egorova in Goryansky *et al.* 1964 and *Cirquella* Fritz, 1993 (as "Genus B Fritz 1993, in press") in the Family Nevadiidae.

Buenellus higginsi Blaker, 1988

Figs 27; 28; 29.1-3

1988 *Buenellus higginsi* sp. nov. Blaker, p. 36, figs 3-6. 1990 *Buenellus higginsi* Blaker, 1988; Peel, fig. 2B. 1993 *Buenellus higginsi* Blaker, 1988; Palmer & Repina 1993, p. 31, fig. 9.6.

Holotype. – MGUH 18.287 from GGU collection 319571, Buen Formation, Sirius Passet, Peary Land (Fig. 28.2).

Figured paratypes. – Damaged complete specimens; MGUH 17.586-17.590, from GGU collection 319571. Damaged cephalon and partial thorax; MGUH 17.585 from GGU collection 319571. All specimens are from the same collection and locality as the holotype.

Other material. – *Buenellus higginsi* is abundant in GGU 319571 from the same locality as the holotype and figured material.

Diagnosis. – As for genus.



Fig. 28. *Buenellus higginsi* Blaker, 1988. Buen Formation. 1, paratype, damaged complete specimen, latex of external mould, dorsal view, MGUH 17.588 from GGU collection 319571, x 1.75. 2, holotype, damaged complete specimen, dorsal view, MGUH 18.287 from GGU collection 319571, x4.

Description. - Cephalon semicircular in outline. Elongate glabella tapers gently forward with rounded anterior; it is of low convexity transversely, whilst sagittally the posterior three-quarters are horizontal on average with the anterior quarter sloping gently downward to the preglabellar field. Occipital ring wide (sag.), horizontal and slightly below level of rest of glabella; sagittal length approximately one-quarter that of glabella. SO moderately concave posteriorly, being of medium depth distally, shallowing over sagittal line. Posterior margin of occipital ring has similar curvature to SO. Weakly developed occipital spine or node. Up to three pairs of glabellar furrows are developed, although on most specimens it is only the posterior pair that are visible. S1 of moderate length, directed moderately backwards, not connected across glabella but joined to axial furrow. S2 shorter than S1, directed backwards at a similar angle and of about equal depth. S3 only observed on one specimen (Fig. 28.2), a shallow expanded furrow shorter than S2. Exsagittal length of lateral glabellar lobes decreases forwards. Glabella defined by narrow (tr.) furrow which is weakly to moderately impressed. Glabella anteriorly separated from border by narrow (sag.) preglabellar field with a sagittal length of about one-fifth that of glabella. Transverse width of intraocular areas between three-eighths and two-fifths of basal glabellar width. Intraocular areas slope gently outward. Palpebral lobes of moderate length (exsag.), narrow (tr.), gently arcuate and centered slightly forward of S1. Palpebral lobes are defined by shallow and narrow (tr.) furrow, or by change in slope of exoskeleton. No apparent differentiation into ocular ridge with the palpebral lobes widening (exsag.) as they approach the glabella. Exsagittal length of lobes approximately two-fifths of sagittal glabellar length. Low narrow (tr.) intergenal ridge extends from posterior tip of ocular lobe backwards at an angle of 70 degrees to border. From the same position on the border a low straight metagenal ridge is directed forward at an angle of about 60 degrees to an exsagittal line towards the glabella, which it joins slightly anteriorly of SO. The two ridges meet at the position of the intergenal spine which is marked by a slight swelling of the border. Extraocular cheeks gently convex (tr.), sloping moderately outwards. Anterior margin of cephalon evenly curved and continuous along short, stout, posterolaterally-directed genal spine. Posterior border directed gently posterolaterally from axis until position of intergenal spine, then slightly anterolaterally to base of genal spine. Weakly defined border of moderate width and border furrow are even less well defined anteriorly and anterolaterally.

Thorax usually formed of 18 segments (but see discussion below) with no macropleural segments. Posterior to the eighth segment the thorax tapers rapidly backwards; over segments 1-8 there is a slight widening of the thorax backwards. Axial rings of moderate convexity (tr.), with axis defined by narrow (tr.) furrow. Posterior margins of axial rings variable from straight transverse to gently concave posteriorly. Lateral margins of axial rings moderately curved outwards. Rings have a median node, often elongated along the sagittal line. Transverse width of ring approximately one-third width of corresponding segment. Pleurae gently sigmoidal in plan view; adaxial half directed gently posterolaterally, abaxial half initially anterolaterally then extended into posterolaterally-directed broad, stout spine. Each pleura marked by wide (exsag.) furrow of medium depth that extends over adaxial half. The anterior ridge extends into a spine on some specimens, whilst the posterior ridge ends at the fulcrum. The more posterior segments have a relatively shorter pleural furrow being only one third the pleural length. Pleurae become directed more strongly posteriorly from the tenth segment backwards. Pleurae very slightly convex (tr.), sloping outwards from axial furrow.

Pygidium usually formed of a single plate that is subtriangular in outline, gently convex (tr. and sag.) and sloping moderately backwards. A transverse furrow that is concave posteriorly and of medium depth, crosses the pygidium.

Sculpture is of fine granules covering all parts of the exoskeleton. This is developed particularly well on a deformed specimen of an incomplete cephalon and thorax (Fig. 29.2), although most specimens do not show any preserved sculpture.

Discussion. – Within the small population available to Blaker (1988) some variability of morphology has been observed (it has not been possible to study the large collections of *Buenellus higginsi* amassed during expeditions to Sirius Passet during 1989, 1991 and 1994). Specimens are flattened, and as the amount of distortion can not be determined, the relative convexities of the exoskeleton are not those of undeformed material. As mentioned in the description, there is variation in the presence and form of glabellar furrows which is interpreted as being mainly due to taphonomic effects. A convex, transverse marking on the axial rings is often apparent; this marking is interpreted as the impression of the underlying articulating half-ring which is visible due to compression of the specimen.

As described, the pygidium is usually composed of a single subtriangular plate bearing a transverse furrow. On at least two specimens, however, (one of which is illustrated in Fig. 28.1) it appears that the final 'thoracic' segment is still retained in the pygidium, despite the considerable sagittal length of the specimens. For these specimens the pygidium is formed of the unreleased segment, bearing short, unfurrowed spines that are directed strongly backwards, and the terminal piece. The plate is separated from the unreleased segment by an incomplete furrow that is represented distally by moderately deep pits. It is noted that these specimens with only 17 segments in the thorax, have sagittal lengths greater than those of several specimens with 18; the condition therefore is not merely a feature associated with immature specimens, but rather with variation within the adult.

Palmer & Repina (1993) considered Buenellus to indi-



Fig. 29. Trilobites from the Buen Formation.

1-3. *Buenellus higginsi* Blaker. 1988. 1, paratype, damaged complete specimen, dorsal view, MGUH 17.587 from GGU collection 319571, x 2.5. 2, paratype, damaged cephalon and partial thorax, dorsal view, MGUH 17.585 from GGU collection 319571. x 2.5. 3, paratype damaged complete specimen, dorsal view, MGUH 17.590 from GGU collection 319571, x 2.8.

4-6. *Olenellus hyperboreus* (Poulsen, 1974). 4, cephalon and partial thorax, dorsal view. MGUH 23232 from GGU collection 271798, x 1.4. 5, cephalon and partial thorax, dorsal view, MGUH 23233 from GGU collection 184219, x 5.3. 6, cephalon, and partial thorax, latex of external mould, MGUH 13.945 from GGU collection 184219, x 3.9.

cate an age within the *Nevadella* Zone of the North American Early Cambrian, an age which is not inconsistent with the occurrence of the contemporaneous *Halkieria* (Conway Morris & Peel, 1995; see also Vidal & Peel 1993); this conclusion is supported here.

Buenellus higginsi, although abundant, is known only from the immediate vicinity of its type locality. Nevertheless, the age interpretation is supported by the distribution of other olenelline trilobites within the Buen Formation in a regional context. The siliciclastic sediments comprising the Buen Formation vary between about 200 m and 500 m in thickness within the area of outcrop in central North Greenland (Higgins et al. 1991a; Ineson & Peel 1997). Olenelline trilobites occur at three general levels. B. higginsi is the oldest known trilobite from North Greenland and occurs near the base of the formation in its northern outcrop in association with the unusually elongate Kleptothule rasmusseni Budd, 1995 and other members of the Sirius Passet fauna (Conway Morris & Peel 1990, 1995; Fig. 3, locality 5). Somewhat above the middle of the Buen Formation in its southern outcrop, near the base of the upper mudstone-dominated unit (Fig. 3, locality 1), a nevadiid described below as Limniphacos perspicullum gen. et sp. nov. occurs together with (and is succeeded by) Olenellus hyperboreus (Poulsen, 1974), the type species of Olenellus (Mesolenellus) Palmer & Repina, 1993, in an occurrence strongly suggestive of the boundary between the Nevadella Zone and the overlying Olenellus Zone (cf. Palmer & Repina 1993). In eastern Peary Land (Fig. 3, localities 3 and 4), Olenellus svalbardensis Kielan, 1960 occurs in the uppermost Buen Formation. Carbonates of the Aftenstjernesø Formation and Kap Troedsson Formation, immediately overlying the Buen Formation, contain fragments of olenellines with the characteristic sculpture of Wanneria (cf. Palmer & Repina 1993: 25; Palmer & Peel 1979: 34; Hurst & Peel 1979: 43); Wanneria has a distribution within the middle Olenellus Zone of Palmer & Repina (1993).

Occurrence in North Greenland. – Lowest Buen Formation (Fig. 3, locality 5). Age: Early Cambrian, "*Nevadella*" Zone.

Genus Limniphacos gen. nov.

Derivation of name. – From the Greek *limne* for 'lake', and *phakos* for 'lens of the eye'.

Type species. - Limniphacos perspicullum sp. nov.

Remarks. - In 1969 geologists of the Greenarctic Consortium collected large numbers of olenellids from black shales occurring in the upper part of the Buen Formation, near the base of the upper mudstone-dominated unit, at Brillesø, north of Jørgen Brønlund Fjord, southern Peary Land (Fig. 3, locality 1). This material was described by Poulsen (1974) as Holmia hyperborea, redescribed herein as Olenellus hyperboreus (Poulsen, 1974). From further collections made primarily by Peel during 1974 and 1978, it was recognised that two olenellid trilobites occur within the black shales, together with a diverse fauna of other invertebrate fossils (Palmer & Peel 1979). Some overlap occurs in the distribution of the two trilobite species, as briefly described by Palmer & Peel (1979). The lowest collections are dominated by a nevadiid characterised by small eyes and an unusual ornamentation which

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occurs together with specimens of *Olenellus hyperboreus* (Poulsen, 1974). Higher levels within the black shales are dominated by *Olenellus hyperboreus*. The nevadiid is here described for the first time; it is noted that the material has previously been recorded as being a species of *Callavia* Matthew, 1897 by Christie & Peel (1977).

Diagnosis. – Nevadiid with conical glabella tapering gently forwards, not reaching border furrow. Glabella with four or five pairs of furrows. Palpebral lobes short (exsag.) and narrow (tr.) being readily distinguished from the short ocular ridges by their greater transverse width. Narrow (tr.) intraocular genae, wide (tr.) extraocular genae. Intergenal and metagenal ridges converge on posterior border at position of small intergenal spine. Genal spines of moderate length, in slightly advanced position. Well-defined wide cephalic border.

Thorax of at least twelve segments with sigmoidallyshaped posterior margin of pleurae, and the articulated part of the thoracic segment less than one-half total width of pleura; pleurae extended into prominent spines. All parts of exoskeleton with a raised reticulate, and granular sculpture.

Discussion. - Ahlberg et al. (1986: 40), in a revision of the genera included within the Holmiidae, noted that there is an apparent core of "closely similar and related genera", namely Holmia Matthew, 1890, Schmidtiellus Moberg in Moberg & Segerberg 1906, Kjerulfia Kiær, 1917 and probably also Andalusiana Sdzuy, 1961. Other genera were thought to be possible candidates for inclusion in this group of somewhat holmiid-like trilobites; Elliptocephala Emmons, 1844 shares with Wanneria a multidenticulate hypostome and the characteristic sculpture of a network with a small node in each mesh. It was noted by Ahlberg et al. (1986) that what is here described as Limniphacos has similar sculpture. It is not clear from their paper whether they considered that Limniphacos might belong to the family or not. The present study of this genus suggests that it does not.

Limniphacos is questionably assigned to the Family Nevadiidae Hupé, 1953 since the genus most closely resembles Nevadella Raw, 1936 from the Lower Cambrian of North America. From that genus it may be distinguished by its considerably shorter palpebral lobes, for species of Nevadella have ocular lobes that extend back to the level of SO. Additionally, intergenal ridges and spines, and metagenal ridges are not developed in Nevadella. Although a complete thorax of Limniphacos is unknown, the unusual characteristics of this genus with the posterior margin of pleurae that are strongly sigmoidal in outline, and with a short articulated part of the pleura, readily distinguish it from Nevadella.

Nevadia Walcott, 1910, from the Lower Cambrian of North America, differs in that its extraocular cheeks are very wide (tr.), the ocular lobes reach back beyond S1, metagenal ridges are not developed, and only three pairs of glabellar furrows mark the glabella. The thorax of *Ne*-



Fig. 30. Trilobites from the Buen Formation.

1, 2, 4, 7, 9-11. Limniphacos perspicullum gen. et sp. nov. 1, paratype, damaged cephalon and partial thorax, dorsal view, MGUH 23221 from GGU collection 271798, x 1.4. 2, paratype, damaged cephalon and partial thorax, dorsal view, MGUH 23220 from GGU collection 271798, x 2.1. 4, holotype, cephalon and partial thorax, latex of external mould, dorsal view, MGUH 23219 from GGU collection 271798. x 2.8. 7, paratype cephalon, dorsal view, MGUH 23224 from GGU collection 270591, x 2.8. 9, paratype cephalon, latex of external mould, dorsal view, MGUH 23228 from GGU collection 271798, x 2.5. 10, paratype cephalon, dorsal view, MGUH 23223 from GGU collection 184002, x 2.8. 11, paratype hypostome, ventral view, MGUH 23222 from GGU collection 271798, x 8.4. 3, 5, 6, 8, 12. Olenellus hyperboreus (Poulsen, 1974). 3. partial cephalon and thorax, dorsal view, MGUH 23234 from GGU collection 271798, x 0.9. cephalon, dorsal view, 5. MGUH 23235 from GGU collection 184219, x 7.7. 6, cephalon, dorsal view, MGUH 23236 from GGU collection 184219, x 7. 8, hypostome, ventral view, MGUH 23242 from GGU collection 271800, x 2.1. 12, hypostome, ventral view, MGUH 23243 from GGU collection 271800, x 4.9.

vadia is known to have up to 28 segments with wide pleurae that have a distally positioned fulcrum, and that extend into long curved spines.

Buenellus Blaker, 1988 has a similarly-shaped glabella, metagenal and intergenal ridges that reach the border at a comparable position, and narrow ocular lobes. *Bue-nellus* is distinguished by the greater length of the ocular lobes, a weakly furrowed glabella, genal spines that are not in an advanced position, and a poorly defined anterior border. The thorax is comparable in the sigmoidal out-

line of the posterior margin of pleurae but the pleural spines of *Buenellus* are shorter, stouter, and the articulated part of the thoracic segment forms a greater relative proportion of the pleura.

Pseudojudomia Egorova *in* Goryansky *et al.* 1964 (see also Palmer & Repina 1993, fig. 10.3) from the Lower Cambrian of Siberia, shows some similarities to *Limniphacos*. It is distinguished by its ocular lobes that reach back beyond the level of S1, a very narrow (tr.) and short (sag.) anterior glabellar lobe, a posterior border that is directed strongly posterolaterally, a poorly-defined cephalic border and metagenal ridges that join the axial furrow at the level of SO.

Limniphacos perspicullum sp. nov.

Figs 30.1, 2, 4, 7, 9-11; 31.1-3

1977 *Callavia* sp.; Christie & Peel, p. 13. 1979 [nevadiid] Palmer & Peel, p. 33.

Derivation of name. – From the Greek perspicullum, 'spectacles' referring to the shape of the palpebral lobes and ocular ridges. Coincidentally, *Limniphacos perspicullum* was discovered from shales at the base of the upper mudstone-dominated unit of the Buen Formation near the lake Brillesø, in the valley of Børglum Elv, southern Peary Land (Fig. 3, locality 1). The name of this distinctively shaped lake is derived from the Danish word for spectacles.

Holotype. – Cephalon and partial thorax; MGUH 23219 from GGU collection 271798 (Fig. 30.4).

Figured paratypes. – Damaged cephalon and thorax; MGUH 23220-23221 from GGU collection 271798. Hypostome; MGUH 23222 from GGU collection 271798. Cephalon; MGUH 23223 from GGU collection 184002, MGUH 23224 from GGU collection 270591, MGUH 23225 from GGU collection 270592, MGUH 23226-23228 from GGU collection 271798.

Other material. - GGU collections 184002, 270591, 270592, 271798.

Diagnosis. - As for genus.

Description. – Cephalon semicircular in outline, being very gently convex transversely and longitudinally. Glabella elongate, gently convex (tr. & sag.), tapering rapidly forwards until level of S1, then more gently anteriorly of S1 with strongly rounded anterior. Due to compression and distortion of specimens there is variation in glabellar outline. Glabella does not reach to anterior border furrow but is separated from it by a narrow (sag.) preglabellar field which is at most one-twelfth of the sagittal glabellar

length. Four or five pairs of glabellar furrows developed, with S4 and S5 often being very weakly impressed. S1 deep, of moderate length and directed backwards at an angle of approximately 65 degrees to an exsagittal line. S1 very slightly curved and connected to axial furrow. Adaxially S1 shallows into diffuse shallow pits that are not confluent across the glabella. S2 considerably shallower than S1, shorter and directed backwards at lower angle. S2 reaches to axial furrow, and is very gently curved. S3 shallower than S2 and directed backwards at similar angle, although more strongly curved; slightly shorter than S2 and reaching axial furrow on most specimens, rarely isolated, and never connected across glabella. S4 very shallow, short and diffuse, situated slightly forwards of ocular ridge termination and joined to axial furrow. In lateral profile glabella rises noticeably from S1, with L1 and the occipital ring averaging horizontal. Over distal one-third SO of similar depth to S1, and directed backwards at about 50 degrees to an exsagittal line. Axial third of SO transverse and shallow. Sagittal length of occipital ring approximately one-seventh that of glabella. Medial part of ring slightly upturned, whilst abaxial one-third is directed strongly anterolaterally at angle of about 65 degrees, so that the lateral parts of the ring lie anteriorly to the adaxial parts of the posterior border. A short median spine is directed upwards and backwards from the posterior margin of the ring. Glabella defined by narrow furrow of variable depth and width, dependent upon amount of deformation. For specimens that are least compressed the axial furrow posteriorly of S1 is shallow, with considerable increase in depth anteriorly of S1 until level of S4. Furrow defining the anterior glabellar lobe is broad, being widest sagittally, and of medium depth. Transverse width of intraocular cheeks narrow, being variable between one-third and one-seventh basal glabellar width (this is interpreted to be a consequence of differential compression of specimens). Intraocular areas very gently convex, sloping slightly adaxially. Palpebral lobes short (exsag.), wide (tr.), strongly arcuate and centred at level of, or slightly anteriorly to, abaxial termination of S2. Palpebral lobes strongly upraised being defined by very shallow furrow, or rapid change in exoskeletal slope. Lateral margins of palpebral lobes approach being vertical. Differentiation into ocular ridge marked by the lower relief of ridges. Exsagittal length of palpebral lobes about one-fifth sagittal glabellar length. Ocular ridges short and straight, defined by narrow furrows. On many specimens a furrow extends from the posterior tip of the palpebral lobe backwards at an angle of about 60 degrees to the posterior border, and marks the position of the intergenal ridge. Faint indications of an intergenal ridge are apparent, however, on some specimens; this is particularly evident close to the posterior border. The interception of the intergenal ridge on the posterior border is marked by a small intergenal spine. From the position of the intergenal spine a very low, straight metagenal ridge is directed towards the glabella, which it reaches at approximately the midpoint of L1. Extraocular cheeks



Fig. 31. Trilobites from the Buen Formation.

1-3. Limniphacos perspicullum gen. et sp. nov. Buen Formation. I, paratype cephalon, dorsal view, MGUH 23227 from GGU collection 271798, x 2.1. 2, paratype cephalon, dorsal view, MGUH 23225 from GGU collection 270592, x 2.1. 3, paratype cephalon, dorsal view, MGUH 23226 from GGU collection 271798, x 2.1.

4-9. Olenellus hyperborea (Poulsen, 1974). Buen Formation. 4, partial cephalon, thorax and pygidium, latex of external mould, dorsal view, MGUH 23234 from GGU collection 271798, x 1.4. 5, cephalon, dorsal view, MGUH 23239 from GGU collection 184002, x 4.2. 6, cephalon, dorsal view, MGUH 23238 from GGU collection 184219, x 3.9. 7, ceph-alon, dorsal view, MGUH 23237 from GGU collection 184219, x 3.2. 8, cephalon, dorsal view, MGUH 23240 from GGU collection 184002, x 4.9. 9, cephalon. dorsal view, MGUH 23241 from GGU collection 184002, x 7.

gently convex (tr.), sloping moderately outwards over adaxial half, and averaging horizontal over distal half, with rapid change in slope between the two. This change in slope is picked out by the sculpture, as described below. Anterior margin of cephalon evenly curved and continuous along moderately long, posterolaterally-directed genal spine. Posterior border about transverse from occipital ring until position of intergenal spine, then directed moderately anterolaterally to base of genal spine. This distal section is either straight or very gently curved, with the genal spines in a slightly advanced position. Wide (sag.) border, gently convex being at its widest posterolaterally, with the posterior border being the narrowest part of the cephalic border. Anterior and posterior border defined by narrow furrow, posterolaterally border defined by subtle change in exoskeletal slope.

Hypostome (Fig. 30.11) subquadrate in outline with sagittal length equivalent to maximum transverse width. Sagittal length of anterior lobe approximately twice that of posterior lobe. Anterior lobe moderately convex transversely, gently convex sagittally, with short maculae posteriorly. Middle furrow continuous, gently concave posteriorly. The posterior lobe is at a lower elevation than the anterior, and slopes rapidly down to border furrow over the posterior half. Border surrounding posterior lobe is narrow and flat sagittally, widening and becoming gently upturned anterolaterally. Anterior wings short.

Thorax formed of at least twelve segments, none macropleural. The thorax widens very slightly over the anterior three segments, whilst more posteriorly there is very gentle taper. Axial rings moderately convex (tr.), with narrow, deep axial furrow. Distal parts of axial rings directed moderately anterolaterally, and marked by shallow furrow at angle of about 65 degrees to the sagittal line. The eleventh and twelfth rings at least, have median spines developed; it is not possible to determine if these are also developed on the other rings. Transverse width of ring approximately one-third width of segment. Anterior three pleurae gently sigmoidal in plan view along posterior margin, posteriorly pleurae becoming more strongly sigmoidal. For anterior pleurae adaxial part directed very slightly posterolaterally and extending into long, slender pleural spine that is directed initially anterolaterally, and then is recurved posterolaterally. For the posterior pleurae the pleural spine forms over two-thirds of the pleura with the adaxial third directed gently posterolaterally. The curvature of the pleural spine is as for the anterior pleurae, but it is noted that for the posterior segments the termination of the pleural spine is slightly forward, or at the level of the posterior margin of the corresponding axial ring, whilst for the anterior three rings the spine tip is behind the posterior margin, with a gradual transition between the two conditions over the middle of the thorax. Each pleurae is marked by a wide (exsag.) furrow of moderate depth that extends over the adaxial half on the anterior-most segments, with this proportion decreasing to less than a third posteriorly, with the genal spine forming the majority of the pleurae. The fulcrum is very short (tr.).

Sculpture of the cephalon is complex; with closelyspaced coarse granules on the occipital ring and L1, smaller, even more closely-spaced granules on L2, and very tightly-spaced fine granules on all parts of glabella anterior of S2. Intraocular cheeks ornamented with coarse widely-spaced granules, with a similar sculpture on the horizontal part of the extraocular cheeks, whilst the adaxial half of extraocular cheeks has fine, closelyspaced granules. Inner part of border sculptured with median-sized granules with progressive increase in density of granules, accompanied by reduction in size towards outer margin. Posterior border with coarse granules adaxially of intergenal spine, abaxially granules decrease in size and are more tightly spaced. Genal spine with sculpture of very fine, closely-spaced granules. A very fine reticulate network covers all parts of the cephalon with each granule enclosed by a polygon. Open polygons (i.e. those not enclosing a granule) occur even in the most densely granulated areas of the genae. All parts of the hypostome have a reticulate ornamentation with coarse granules on the anterior of the posterior lobe, with a fining of granule size towards the posterior margin. Medium granules on anterior lobe. A polygonal network is also developed on the thorax, with the medial parts of the axial rings sculptured with medium granules. The pleurae have very coarse granules adaxially that grade distally into finer, more closely-spaced granules over the pleural spine.

Occurrence in North Greenland. – Base of the upper mudstone-dominated unit of the Buen Formation, (Fig. 3, localities 1 and 6). Age: Early Cambrian, boundary between the "*Nevadella*" Zone and the *Olenellus* Zone.

Superfamily Olenelloidea Walcott, 1890 Family Olenellidae Walcott, 1890

Diagnosis. – After Bergström (1973b: 312). Olenelloidean trilobites with fairly large frontal glabellar lobe; narrow (tr.) interocular area; metagenal spines distally positioned; pleural furrows generally extending through pleural spines; third thoracic segment may be macropleural; hypostome commonly multidenticulate.

Remarks. – The Olenellidae is a uniform group within which classification is difficult since morphologic variation frequently exhibits no distinguishable gaps (Bergström 1973b: 313; Palmer & Repina 1993: 8). Palmer & Repina (1993) recently presented a comprehensive classification of the Olenellidae, including the recognition of 5 subgenera of *Olenellus*. The type species of one of these subgenera (*Mesolenellus* Palmer & Repina, 1993) is *Holmia hyperborea* Poulsen, 1974 from the Buen Formation of North Greenland, described below as *Olenellus hyperboreus*. Subgenera of *Olenellus* are not employed in the present context, for which reason the present conservative classification follows that of Bergström (1973b).

Genus Olenellus Hall, 1861

Discussion. – The authorship of *Olenellus* was recently discussed by Whittington (1989: 114; cf. Palmer & Repina 1993: 22).

Fritz (1972) discussed *Olenellus* and included species formerly assigned to *Paedeumias* Walcott, 1910 and *Fre*-

montia Raw, 1936; the synonomy of *Fremontia* and *Olenellus* had been suggested also by Robison & Hintze (1972). *Mesonacis* Walcott, 1885 has also been widely regarded as a synonym of *Olenellus* (cf. Resser & Howell 1938). Palmer & Repina (1993) recognised *Paedeumias* and *Mesonacis* as subgenera of *Olenellus sensu lato*, together with the new subgenera *Angustolenellus* and *Mesolenellus*. *Fremontia* was considered to be a junior synonym of *Olenellus* (*Mesonacis*) by Palmer & Repina (1993).

Bergström (1973b: 312) included *Sinskia* Suvorova in Chernysheva 1960 as a synonym of *Olenellus*. Subsequently, Repina (1979b) considered *Sinskia* to be a valid member of the family Nevadiidae, subfamily Judomiinae Repina, 1979b which subfamily Palmer & Repina (1993) elevated to a family of the superfamily Fallotaspidoidea; this assignment to the Judomiidae is supported here.

Type species. – *Olenus thompsoni* Hall, 1859, from the Lower Cambrian strata of Parker's Quarry, near Georgia, Vermont, U. S. A. Palmer & Repina (1993: 22) indicated that the holotype is lost.

Diagnosis. – After Fritz (1972: 11). Cephalon semicircular in outline. Three pairs glabellar furrows. Occipital spine very short. Ocular lobes arcuate. Interocular area considerably narrower (tr.) than extraocular genal area. Border extends back without appreciable change in curvature to genal spines. Posterior border marked by slight swelling or very small spine at intergenal position.

Thorax of up to 15 segments in the prothorax, the third macropleural. Pygidium very small.

Olenellus cf. O. gilberti Meek in White & St. John, 1874

Fig. 55.10, 12, 13

- cf. 1874 Olenellus gilberti Meek in White & St. John, p. 7.
- cf. 1979 *Olenellus gilberti* Meek; Palmer in Palmer & Halley, p. 71, pl. 3, figs 6-13.

Type material. – Type series USNM 15411a-c in the Natural History Museum, Smithsonian Institution, Washington D. C., from the Lower Cambrian Pioche Shale, Pioche, Lincoln County, Nevada, U. S. A.

Figured material. – Cephala; MGUH 23229-23231 from GGU collection 270584.

Other material. - GGU collection 270568.

Remarks. – Due to their occurrence in coarse sandstone the specimens are indifferently preserved and are only compared to *O. gilberti*.

The glabella is elongate being separated from the frontal border by a narrow preglabellar field, the frontal lobe is subcircular in outline and is distinguished from the extraocular cheeks by an abrupt change in exoskeletal slope; three pairs of glabellar furrows are developed whilst the occipital furrow is deep at the sides of the glabella and is not connected across the top of glabella. The ocular lobes are long, slender (tr.) and the interocular cheek is only about as wide as the ocular lobe at level of S1. The extraocular cheek is broad and gently convex (tr.). The ocular lobes are of greater sagittal length than specimens more typical of the species, although it was noted by Palmer (in Palmer & Halley 1979: 72) that lobe length in *O. gilberti* is variable.

Occurrence in North Greenland. – Sæterdal Formation (Fig. 8B). Age: Early Cambrian, *Olenellus* Zone.

Olenellus hyperboreus (Poulsen, 1974)

Figs 29.4-6; 30.3, 5, 6, 8, 12; 31.4-9

1974 Holmia hyperborea n. sp., Poulsen, p. 84, pl. 1, figs 4-7; pl. 2, figs 1-6; pl. 3, figs 1-8.

1977 Holmia hyperborea; Christie & Peel, p. 13.

1979 *Holmia hyperborea* Poulsen, 1974; Palmer & Peel, p. 33.

1986 Holmia hyperborea; Ahlberg et al., p. 41.

1993 Olenellus hyperboreus; Vidal & Peel, p. 6.

1993 Olenellus (Mesolenellus) hyperborea Poulsen, 1974; Palmer & Repina, p. 22, fig. 3.7.

Type material. – Holotype, MMH 13.008 from GGU collection 100824, an external mould of a complete specimen collected from black shales at the base of the upper mudstone-dominated unit of the Buen Formation at Brillesø, Børglum Elv, Peary Land, North Greenland. Specimen figured by Poulsen (1974, pl. 1, fig. 4).

Figured material. – Complete specimen; MGUH 13.945 from GGU collection 184219 (specimen figured by Palmer & Repina 1993, fig. 3,7, but by lighting the external mould from the lower right to create a photographic replica). Cephalon and partial thorax; MGUH 23232, 23234 from GGU collection 271798, MGUH 23233 from GGU collection 184219. Cephalon; MGUH 23235-23238 from GGU 184219, MGUH 23239-23241 from GGU collection 184002. Hypostome; MGUH 23242-23243 from GGU collection 271800.

Other material. – GGU collections 184002, 184007, 184219, 218637, 270591, 270592, 271700.

Remarks. – The assignment of *Holmia hyperborea* to *Olenellus* was discussed by Ahlberg *et al.* (1986: 41). They noted that the assignment of the Greenland material by

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Poulsen (1974) had been based mainly on small specimens, whilst larger specimens are decidedly more like *Olenellus*. Palmer & Repina (1993) made *H. hyperborea* type species of a new subgenus, *Mesolenellus*, of *Olenellus*.

Emended diagnosis. – After Poulsen (1974: 84). Cephalon of low convexity (tr. & sag.), semicircular to subelliptical in outline, with well-advanced genal spines. Cephalic border narrow; palpebral lobes long (exsag.) and wide (tr.). Hypostome with long (sag.) anterior lobe, posterior border with five pairs of spines and medial spine. Thorax of twenty segments, 14 prothoracic segments all with posteriorly situated median axial node. Six opisthothoracic segments, anterior-most bearing long (sag.) axial spine, posterior five without axial node. Simple semicircular pygidium formed of a single plate.

Description of hypostome. – Middle body of hypostome ovate in outline, anterior lobe gently convex (tr. & sag.) with sagittal length approximately five times that of posterior lobe. Maculae moderately deep and wide distally, joined across axial line by very shallow furrow. Wide (sag.), flat posterior border weakly defined by shallow furrow. Posterior border with five pairs of marginal spines, and a single median spine. Discussion. – Poulsen (1974: 84) described the cephalon, thorax and pygidium. However, examination of material collected subsequently has revealed a number of discrepancies in the original description. Poulsen (1974) described the occipital furrow (SO) and the anterior pair of glabellar furrows (S3) as being the only pairs to be joined across the axial line. It is now known that S2 is also sometimes joined across the axial line.

The thorax does not consist of 16 segments as described by Poulsen, but rather 20 of which 14 form the prothorax and 6 the opisthothorax. The third segment of the prothorax is macropleural, and the thorax does not therefore attain its greatest width at the fifth segment as stated by Poulsen. All axial rings in the prothorax possess a short axial spine or node, situated close to the posterior margin. As was noted by Poulsen (1974), at least one of the posterior segments bears a longer axial spine. The material now available shows such a spine to be developed only on the anteriormost segment of the opisthothorax. The pygidium although small, is not minute as described by Poulsen (1974), and is formed of a single plate that is semicircular in outline.

A sculpture of reticulate ridges and indistinct granules on the cephalic genae was noted by Poulsen (1974). Sim-



Fig. 32. *Olenellus svalbardensis* Kielan, 1960. Buen Formation. 1, cephalon and partial thorax, dorsal view, MGUH 23248, x 2. 2, damaged complete specimen, dorsal view, MGUH 23429, x 2. Both from GGU collection 256959.

ilar sculpture is now also recognised on the thoracic axial rings and anterior pleural bands, with similar subdued sculpture on the posterior pleural bands and hypostome.

Occurrence in North Greenland. – Buen Formation (Fig. 3, collection localities 1, 2 and 6). Age: Early Cambrian, boundary between the "*Nevadella*" Zone and the *Olenellus* Zone.

Olenellus svalbardensis Kielan, 1960

Figs 32-34

- 1960 Olenellus svalbardensis n. sp. Kielan, p. 84, pls 1-3, pl. 4, figs 1-2.
- 1974 Olenellus cf. svalbardensis Kielan, 1960; Poulsen, p. 82, pl. 1, figs 1-3.



Fig. 33. *Olenellus svalbardensis* Kielan, 1960. Buen Formation. 1, thorax and pygidium, dorsal view, MGUH 23254 from GGU collection 256959, x 2. 2, cephalon and partial thorax, dorsal view, MGUH 23250 from GGU collection 271048, x 1.75. 3, cephalon and partial thorax, dorsal view, MGUH 23252 from GGU collection 271048, x 1.5. 4, partial cephalon and thorax, dorsal view, MGUH 23246 from GGU collection 256959, x 2. 5, cephalon and partial thorax, dorsal view, MGUH 23247 from GGU collection 256959, x 3. 6, cephalon and partial thorax, dorsal view, MGUH 23245 from GGU collection 256959, x 2.25.



Fig. 34. *Olenellus svalbardensis* Kielan, 1960. Buen Formation. 1, cephalon and partial thorax, latex of external mould, MGUH 23253 from GGU collection 271048, x 1.9. 2, cephalon and partial thorax, dorsal view, MGUH 23244 from GGU collection 256959, x 1.9. 3, cephalon and partial thorax, latex of external mould, MGUH 23251 from GGU collection 271048, x 1.9.

1977 Olenellus svalbardensis Kielan, 1960; Orlowski in Birkenmajer & Orlowski, p. 176, pl. 1, figs 1-7.

Type material. – Holotype cephalon (Sv-I/14) from Lower Cambrian Slaki Series (= Slaklidalen Limestone Formation of Birkenmajer & Orlowski 1977), Hornsund, Vestspitsbergen. Housed in the Laboratory of Geology, Polish Academy of Sciences, Cracow, Poland.

Figured material. – Cephalon and partial thorax; MGUH 23244-23249 from GGU collection 256959, MGUH 23250-23253 from GGU collection 271048. Thorax and pygidium; MGUH 23254 from GGU collection 256959.

Other material. - GGU collections 256959 and 271048.

Emended diagnosis. – After Kielan (1960: 85). Long (exsag.) ocular lobes extending from S3 to level of SO. Weakly developed glabellar furrows. Interocular area very narrow (tr.). Preglabellar field developed. Occipital ring with small median node on posterior margin. Genal spines in slightly advanced position. Prothorax of 15 segments; posteriorly situated median spine on axial rings. Extraocular cheeks with anastomosing caeca.

Description. – Cephalon semicircular in outline, gently convex transversely and longitudinally. Elongate glabella expands forwards of SO to sharply rounded anterior. Glabella separated from anterior border furrow by preglabellar field of variable sagittal length; generally short. Narrow (sag.) occipital ring gently convex (tr.), in lateral pro-

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file gently upturned posteriorly with small median node on posterior margin; sagittal length approximately oneeighth that of glabella. SO gently concave posteriorly, of greatest depth distally, becoming very shallow over sagittal line. Glabellar furrows generally not apparent although on rare specimens up to three pairs visible. All pairs shallow, of moderate length, straight and directed moderately backwards; not connected across glabella or to axial furrow. Laterally, glabella defined by narrow furrow that is well-impressed and continuous with a shallower preglabellar furrow.

Transverse width of interocular cheeks variable between one-third and one-half basal glabellar width. Interocular cheeks horizontal or sloping gently inwards; at higher elevation than extraocular cheeks. Long (exsag.) palpebral lobes of moderate width (tr.), with reduction in width posteriorly, strongly arcuate and terminating at approximately the level of SO. Lobes very strongly arched transversely with lateral margins that approach being vertical. Palpebral furrow deep and of moderate width (tr.), occasionally shallowing posteriorly. The outer margin of the lobe is defined by a very marked change in exoskeletal slope. The lobe is unfurrowed with exsagittal length about one-half sagittal glabellar length. Extraocular cheeks of low convexity, slope very slightly outwards. Anterior margin of cephalon evenly curved and continuous along long, slender, posteriorly-directed genal spine which is in a slightly advanced position. Cephalic border narrowest in front of glabella, widening posterolaterally and attaining maximum width at genal angle, defined by narrow furrow. Border gently concave with shallow median furrow. Posterior border curved gently to moderately anterolaterally over distal two-thirds, approximately transverse adaxially.

Thorax of at least 17 segments of which 15 form the prothorax and two are in the opisthothorax. The third segment is macropleural, although only weakly so for some specimens. Axial rings of moderate convexity (tr.), sloping moderately down from anterior to posterior with small, posteriorly situated median node. Axial furrow narrow (tr.) and well-impressed. Posterior margins of axial rings variable from gently concave posteriorly to straight transverse. Short (tr.) pleurae extend into long, gently curved pleural spines that are posterolaterally directed. Pleural furrows wide (exsag.) and of moderate impression, deepest distally and continuous onto spines as very shallow furrow. The two segments known in the opisthothorax have very reduced pleural spines and axial rings without median nodes.

The pygidium is formed of a moderately convex (tr. & sag.) single plate that is subtriangular in outline.

Sculpture has only been observed on the extraocular cheeks and genal spines. For the cheeks sculpture consists of anastomosing caeca that vary in relief and width throughout the population. This appears to be related to size, with small specimens having very low, narrow caeca and larger specimens caeca that are wider and have stronger relief. Some of the smallest specimens have extraocular cheeks that lack caeca. On the genal spine, and the posterolateral part of the cephalic border terrace ridges form the sculpture.

Discussion. – Within the population available for study a considerable range of morphology has been observed. This range is increased because the specimens are flattened and distorted to varying degrees which has produced variability in glabellar convexity and outline. A more-or-less complete gradation is known, however, between the two ends of the morphological spectrum, without any obvious breaks at which species might be defined. The description has been based on the least deformed material but, as the amount of deformation can not be determined, the relative convexities of the exoskeleton are not those of undeformed material.

Kielan (1960: 86) described the fifteenth thoracic segment as bearing a "... long median spine, directed backwards". Three specimens have such a spine within the population studied here, but the development is from the fourteenth axial ring and, for these specimens, axial nodes are additionally very low or absent. The presence or absence of this thoracic spine could be used to distinguish a separate species. However, in all other features of morphology the specimens are identical; they may represent a dimorphic pair.

Poulsen (1974: 82) believed that the material he described from eastern Peary Land was conspecific with *Olenellus svalbardensis* Kielan, 1960 but refrained from a definite assignment until further material was available. The specimens were preserved as weathered fragments in slate with irregular cleavage from collections made more than 20 years previously by Johannes C. Troelsen.

Christie & Ineson (1979) reported large collections of trilobites made during 1978 from localities in the general area of G. B. Schley Fjord, eastern Peary Land, which is the material described here. Palmer & Peel (1979: 33) considered there to be at least three olenellid taxa present, as well as *Serrodiscus*, although it was admitted that the material had not been closely studied. As stated above, the specimens have undergone varying degrees of deformation, in part concerning their orientation relative to cleavage. In consequence, it is considered that only a single species is represented.

Poulsen (1974) considered that the occurrence of *Ole-nellus svalbardensis* in both North Greenland and Spitzbergen might well be expected due to the proximity of the two areas during the Early Cambrian. This proximity has subsequently been reaffirmed in a number of palaeogeographical reconstructions for this time period (see for example Scotese *et al.* 1979; Scotese & McKerrow 1990).

Occurrence in North Greenland. – Uppermost beds of the Buen Formation (Fig. 3, localities 3 and 4). Age: Early Cambrian, *Olenellus* Zone.

Olenellus cf. O. truemani Walcott, 1913

Figs 35-37; 38.6; 59.2, 5

- cf. 1913 Olenellus truemani Walcott, p. 316, pl. 54, figs 2-10.
- cf. 1916 Olenellus truemani Walcott, p. 253, pl. 17, figs 2-10.
- cf. 1972 Olenellus truemani Walcott; Fritz, p. 16, pl. 9, figs 1-14.

Figured material. – Cephalon and thorax; MGUH 23255 from GGU collection 315087. Cephalon; MGUH 23256-23260 from GGU collection 271755, MGUH 23261 from GGU collection 301336, MGUH 23262 from GGU collection 298537, MGUH 23263 from GGU collection 315090, MGUH 23264 from MGUH 298979, MGUH 23265-23266 from GGU collection 315049, MGUH 23267-23271 from GGU collection 315140, MGUH 23272-23276 from GGU collection 315174, MGUH 23277 from GGU collection 315049, MGUH 23279 from GGU collection 315049, MGUH 23279 from GGU collection 315049, MGUH 23279 from GGU collection 315174, MGUH 23280 from GGU collection 271756.

Other material. - GGU collections 225703, 225704, 271755, 271756, 298537, 301336, 301338, 301346, 315049, 315087, 315090, 315093, 315112, 315140, 315174.

Fig. 35. Olenellus cf. O. truemani Walcott, 1913. Henson Gletscher Formation. 1, cephalon and thorax, ventral view, photograph, field MGUH 23255 from GGU collection 315087, x 0.5. 2, thorax, ventral view; MGUH 23255 from GGU collection 315087, x 0.7. cephalon, dorsal view, MGUH 23259 from GGU collection 271755, x 2.8. 4, cephalon, partially exfoliated, dorsal view, MGUH 23260 from GGU collection 271755, x 2.8. 5, damaged cephalon, partially exfoliated, dorsal view, MGUH 23261 from GGU collection 301336, x 1.4. 6, damaged cephalon, partially exfoliated, dorsal view, MGUH 23262 from GGU collection 298537, x 1.4. 7, damaged cephalon, dorsal view, MGUH 23256 from GGU collection 271755, x 1.4. 8, damaged cephalon, dorsal view, MGUH 23257 from GGU collection 271755, x 1.75. 9, damaged cephalon, dorsal view, MGUH 23258 from GGU collection 271755, x 2.1.



Description. – Semicircular cephalon gently convex (tr. & sag.), with maximum transverse width almost twice sagittal length. Marginal curvature of cephalon continuous onto slender genal spine of moderate length, located very slightly in advance of posterolateral cephalic corner.

Posterior margin directed gently posterolaterally from occipital ring to position of intergenal swelling, then more steeply backwards for short distance and finally forwards to genal spine base. Intergenal spines very small and slender, posterolaterally directed; absent on larger

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Fig. 36. *Olenellus* cf. *O. truemani* Walcott, 1913. Kap Troedsson Formation. 1, meraspid cephalon, stage IV, dorsal view, MGUH 23271 from GGU collection 315140, x 16. 2, meraspid cephalon, stage IV, dorsal view, MGUH 23269 from GGU collection 315140, x 18. 3, meraspid cephalon, stage IV, dorsal view, MGUH 23270 from GGU collection 315140, x 17.5. 4, meraspid cephalon, stage IV, dorsal view, MGUH 23276 from GGU collection 315140, x 15.5. 5, meraspid cephalon, stage IV, dorsal view, MGUH 23276 from GGU collection 315140, x 15.5. 5, meraspid cephalon, stage IV, dorsal view, MGUH 23276 from GGU collection 315174, x 13. 6, meraspid cephalon, stage IV, dorsal view, MGUH 23276 from GGU collection 315174, x 9, meraspid cephalon, stage IV, dorsal view, MGUH 23274 from GGU collection 315174, x 9. 8, meraspid cephalon, late stage IV, dorsal view, MGUH 23267 from GGU collection 315174, x 8. 9, meraspid cephalon, late stage IV, dorsal view, MGUH 23267 from GGU collection 315140, x 8.

specimens (where sag. length >10 mm). Narrow, gently convex cephalic border, well-defined around entire cephalic margin by shallow border furrow. Glabella gently convex (tr. & sag.), elongate and separated from frontal border by wide (sag.) preglabellar field. Frequently a low and narrow (tr.) median ridge extends from the anterior glabellar lobe to the cephalic border. Anterior glabellar lobe subtriangular to subconical in outline, slightly inflated above posterior part of glabella, and strongly inflated above adjacent extraocular checks. Frontal lobe defined by narrow ridge and furrow; furrow consistently well-impressed posterolaterally and anteriorly, frequently shallow or absent anterolaterally resulting in distinct tripartite division. Ridge separated from extraocular cheek by

change in exoskeletal slope. Posterior part of glabella defined laterally by very shallow furrows between SO and S1, deeper forwards of S1. Glabellar sides converge gently forwards between SO and S1, with rapid expansion forwards of S1 until level of S2. Three pairs of glabellar furrows; S1 straight and directed gently backwards, reach to axial furrow but not joined across glabella. On several specimens, shallow, yet distinct, U-shaped furrows connect the adaxial termination of S1 with approximately its midpoint (Fig. 35.6). S2 short and arcuate, averaging transverse or directed weakly backwards, not connected across glabella. Joined to axial furrow by very shallow, posterolaterally directed furrow. S3 directed posteriorly at higher angle than S1, of similar depth to S2 but longer. S3 reaches across glabella, being joined by shallow furrow. S3 confluent with a furrow that is possibly the axial, this in turn joins with a furrow defining the adaxial margin of the palpebral lobe. Occipital furrow (SO) represented distally by deep, short, transverse furrows that are rarely connected across glabella. Occipital ring gently convex transversely, with median node adjacent to posterior margin. Sagittal length of occipital ring approximately one-sixth that of glabella. Arcuate palpebral lobes wide (tr.) and long (exsag.), tapering slightly posteriorly. Line connecting posterior terminations passes over the occipital ring. A moderately deep intraocular furrow parallels the outer margin of the palpebral lobe along its entire length, and is distant from it by a width (tr.) about equal to its own. Width (tr.) of interocular cheek about equal to that of ocular lobe at level of S1, narrowing to about half this width posteriorly. Extraocular cheek very gently convex (tr. & sag.), of moderate width (tr.).

Hypostome (Fig. 37.3, 6) with long (sag.) and inflated anterior lobe of middle body. Outline of anterior lobe rather pear-shaped, lobe with deep and narrow maculae that are connected across the axial line by a very shallow furrow. Posterior lobe strongly crescentic in outline and very short (sag.). Posterior border defined axially by shallow furrow that narrows anterolaterally. Border with 6 pairs of short, stout spines. Spacing between posterior pair of border spines increases with hypostomal sagittal length.

Thorax with 14 prothoracic segments, the third macropleural and the fourteenth with a very long (sag.), slender axial spine. Opisthothorax poorly known, but formed of at least 5 segments. The thoracic axis tapers gently back-



Fig. 37. *Olenellus* cf. *O. truemani* Walcott, 1913. Kap Troedsson Formation (1, 2, 6) and Henson Gletscher Formation (3-5). 1, meraspid cephalon, stage V, dorsal view, MGUH 23273 from GGU collection 315174, x 7.5. 2, meraspid cephalon, stage V, dorsal view, MGUH 23264 from GGU collection 298979, x 7. 3, hypostome, ventral view, MGUH 23278 from GGU collection 315049, x 3.5. 4, holaspid cephalon, dorsal view, MGUH 23265 from GGU collection 315049, x 2.5. 5, holaspid cephalon, dorsal view, MGUH 23266 from GGU collection 315049, x 3.5.

wards, and is laterally defined by shallow furrows. The pleurae are straight and transverse over most of their length with only the very distal part directed obliquely backwards, and extending into a long and slender, gently curved spine. There is a notable progressive increase in spine length from the third to the tenth segment. Pleural furrows wide (exsag.), and of moderate depth, not extending onto pleural spines. Ventral preservation of the thorax shows there to be short, stout apodemes at the posterolateral corners of all axial rings. The pygidium is unknown.

Sculpture of the cephalon consists of a raised polygonal network of ridges on all parts except the cephalic border on which terrace ridges are developed. Additionally the extraocular cheeks often have strongly-developed radiating caeca. For the largest cephalon (transverse width 147 mm) sculpture of the border is more variable; on the inner half of the broad, convex cephalic border the reticulate sculpture continues across from the extraocular cheeks, whilst the outer half has small broken terrace ridges and irregularly distributed tubercles. A reticulate sculpture is also developed on the thorax.

The specimen of the most complete thorax is of note for the pleural regions differ for the eighth segment. As observed from the ventral side (Fig. 35.1) the right-hand side pleural spine is short and broad, with the pleural furrow extending almost to the tip of the spine. For the lefthand side the pleural region is of more normal aspect with a considerably longer and more slender spine. As there is no evidence of injury this is concluded to be a pathological feature.

Ontogeny. – A number of specimens have been identified that represent the late meraspid and early holaspid developmental stages of *Olenellus* cf. *O. truemani*. Palmer (1957) recognised five developmental stages in the growth sequence of *Olenellus gilberti* Meek in White & St. John 1874 of which correlatives of stages IV and V have been identified in the North Greenland material of *Olenellus* cf. *O. truemani*.

As defined by Palmer (1957: 118), stage IV is characterised by the development of two pairs of well-developed cephalic spines (genal and intergenal). The earliest developmental stage identified from North Greenland is approximately at the midpoint of stage IV (Fig. 36.1) when the transverse width of the posterior margin of the cephalon becomes greater than the sagittal length, and intergenal spine length is greater than for the genal spines. For these specimens the glabella is parallel-sided or tapered gently forwards, the occipital ring is developed and anteriorly there are four lobes defined. The cephalic border is continuous along all margins, and there is a wide (sag.) preglabellar field. Interocular and extraocular cheeks are of about the same width at the level of S1, and the ocular lobes are wide (tr.).

Throughout stage IV the progression is towards reduction of the intergenal spines and by the close of stage IV the intergenal spines are shorter than the genal spines (Fig. 36.8, 9), and the extraocular cheeks have greater transverse width than the interocular. The cephalon is semicircular in outline, and the posterior margin is straight; other morphology is unchanged, except for the expansion of the anterior glabellar lobe.

Stage V is denoted by specimens in which the intergenal spines are reduced to nodes (Fig. 37.2); a feature taken by Palmer (1957) to indicate an adult specimen.

Discussion. - Palmer & Repina (1993) considered Olenellus truemani to be a member of their subgenus O. (Olenellus). The described material from North Greenland shows most similarity with topotype material of Olenellus truemani Walcott, 1913 described by Fritz (1972) from the Lower Cambrian Sekwi Formation, Mackenzie Mountains, North-western Canada. This Canadian material is characterised by the development of a parafrontal band, wide (tr.) extraocular cheeks and a reticulate sculpture on all parts of the cephalon. The most notable difference is that the palpebral lobes in O. truemani are relatively shorter, generally terminating at about the level of SO, although small specimens have palpebral lobes that are of comparable length (see Fritz 1972, pl. 9, fig. 7). Furthermore, the glabella of O. truemani terminates in close proximity of, or adjacent to, the cephalic border furrow, whereas in the specimens from North Greenland there is a wide (sag.) preglabellar field and the anterior glabellar lobe is of more conical outline. Differences in length of the preglabellar field when compared to the type material were also noted by Hu (1971) in an account of O. truemani from Mexico, with Hu concluding that these were due to preservation (see Hu 1971: 77).

It is possible that material described here from North Greenland should be assigned to O. truemani, with differences in cephalic morphology possibly being explained by geographical variation within the species. However, the ontogenetic sequence described above for the North Greenland material is not consistent with that described for O. truemani by Hu (1971). The late meraspid stages described by Hu (1971) were correlated by him to Palmer's (1957) stages III and IV, and differ from the material from Greenland in a more subquadrate outline, ocular lobes that are almost parallel to an exsagittal line, and an anterior lobe that is very flat across its anterior margin and is separated from the anterior border by a narrower preglabellar field. Early holaspid stages illustrated by Hu (1971, pl. 8) also differ since the genal spines are in an advanced position, intergenal spines are well-developed and the anterior glabellar lobe is strongly rounded as opposed to the conical outline in Olenellus cf. O. truemani.

The material from North Greenland also has some similarities with *Olenellus simplex* which Poulsen (1932) described from the Lower Cambrian Ella Island Formation of North-East Greenland. This species also has a reticulate sculpture although many of the polygons have a central granule, particularly those on the extraocular cheek. *O. simplex* also differs in that the interocular cheeks are very narrow (tr.), the anterior glabellar lobe is broadly rounded without a parafrontal band, palpebral lobes are shorter (exsag.) and the glabella does not expand significantly forwards of S1.

Caeca on the extraocular cheeks of olenellids were discussed by Öpik (1961: 418) as being part of the alimentary apparatus. Subsequently Jell (1977) proposed the recognition of four distinct types of caeca, with those on olenellids being of Type 4. Caeca of this type are extremely narrow and do not end blindly; they continue into the border and anastomose regularly. Jell (1977) suggested the caeca to be the external representation of 'auxiliary respiratory systems'.

Parafrontal band is a term introduced by Hupé (1953: 263) who interpreted it as being a vestige of a segment, the pleurae of which are observed in the ocular ridges. As noted by Öpik (1961: 425), this interpretation can not be correct for the parafrontal band is not part of the glabella, but rather the extraocular cheeks. Öpik speculated that the parafrontal band was a duct that connected the left and right genal caecal glands and proposed that it may have served a special function such as the maintenance of pressure in the cheeks and eyes. Jell (1977: 256) suggested a more plausible function, namely that the course of the intermediate collecting vessel of the respiratory bed is marked by the parafrontal band, with this extending from one palpebral lobe to the other.

In 1986, Blaker described the present species as having a 'Wanneria'-type sculpture, whilst other characteristics of the cephalon were inconsistent with an assignment to that genus. The comparison with Wanneria sculpture is now recognised as being incorrect. As was discussed by Palmer (1964: F4), fragments of Wanneria exoskeleton when viewed from the ventral side show a series of perforations that exactly parallel the pattern of the reticulate ridges on the dorsal surface. Such an exoskeletal structure has not been observed in the specimens of Olenellus cf. O. truemani from North Greenland. However, tiny fragments of exoskeleton from the base of the Aftenstjernesø Formation in southern Peary Land preserve the series of perforations characteristic of Wanneria (Palmer & Peel 1979: 34).

Occurrence in North Greenland. – Henson Gletscher Formation, collection localities 1 and 6 (see Figs 8A, 10, 11). Kap Troedsson Formation, collection localities 2 and 5 (see Figs 6, 7). Age: Early Cambrian, *Olenellus* Zone.

Olenellus sp. A

Fig. 38.1-5

Figured material. – Cephalon; MGUH 23283-23284 from GGU collection 315140, MGUH 23285-23286

from GGU collection 298979. Hypostome; MGUH 23287 from GGU collection 298979.

Other material. - GGU collections 298979 and 315140.

Description. – Cephalon similar to that of *Olenellus* cf. *O. truemani* with the following differences: 1, anterior glabellar lobe more rounded at front, and of more bulbous appearance; 2, glabella consistently terminates in close proximity to the cephalic border furrow; 3, palpebral lobes more strongly arcuate; 4, narrower (tr.) extraocular cheeks that are moderately convex and slope strongly downwards; 5, cephalic border considerably wider and strongly convex in cross-section, very wide posterolaterally and continuous with very long, stout genal spines; 6, border defined by deep and narrow furrow; 7, sculpture of terrace ridges on lateral border and genal spines, glabella with Bertillion pattern of very low ridges; 8, intergenal spines situated closer to axial furrows.

The hypostome (Fig. 38.5) that is tentatively assigned to this species differs considerably from that of *Olenellus* cf. *O. truemani* since the sculpture is of widely-spaced, coarse granules.

Discussion. – Specimens assigned to this species and also *Olenellus* cf. *O. truemani* occur together in three samples from the Kap Troedsson Formation, and illustrate a particularly common problem in olenellid taxonomy. As was discussed in some detail by Palmer (in Palmer & Halley 1979: 66), narrow-bordered and wide-bordered olenellids that have essentially the same axial cephalic morphology are frequently found in association. Taxonomic categorisation of these forms has ranged from separate genera (*Paedeumias* and *Olenellus*) to variants of a single species. The case for separate genera has long lacked support in the literature, and the suppression of *Paedeumias* was widely accepted. As discussed above, however, Palmer & Repina (1993) advocated reinstatement of *Paedeumias* as a subgenus of *Olenellus*.

The suggestion that the narrow-bordered and widebordered forms are variants of a single species can not readily be applied or argued for the present material, as there are no transitional forms. Palmer (in Palmer & Halley 1979) believed the more realistic taxonomic choice to be between interpreting narrow-bordered and wide-bordered forms as congeneric species, or as subspecific, perhaps sexual dimorphic variants. The material from the Kap Troedsson Formation suggests separate congeneric species but for further discussion of the question of dimorphism see Palmer (in Palmer & Halley 1979: 67).

Occurrence in North Greenland. – Kap Troedsson Formation, collection locality 2 (Figs 6, 7). Age: Early Cambrian, *Olenellus* Zone.















Fig. 38. Lower Cambrian trilobites.

1-5, *Olenellus* sp. A. Kap Troedsson Formation. 1, cephalon, partially exfoliated, dorsal view, MGUH 23283 from GGU collection 315140, x 6. 2a, b, cephalon, partially exfoliated, dorsal and lateral views, MGUH 23286 from GGU collection 298979, x 5. 3, damaged cephalon, partially exfoliated, dorsal view, MGUH 23285 from GGU collection 298979, x 4.5. 4a, b, damaged cephalon, partially exfoliated, dorsal and lateral views, MGUH 23284 from GGU collection 315140, x 6.5. 5, hypostome, partially exfoliated, ventral view, MGUH 23287 from GGU collection 298979, x 6.5.

6. Olenellus cf. O. truemani Walcott, 1913. Henson Gletscher Formation. 6a, damaged cephalon, partially exfoliated, dorsal view, MGUH 23263 from GGU collection 315090, x 1.5. 6b, as above, enlargement to show sculpture of cephalon, x 6.

Olenellus sp. B

Fig. 26.9, 11

Figured material. – Partial cephalon and thorax; MGUH 23288 from GGU collection 319742. Partial cephalon; MGUH 23289 from GGU collection 319757.

Other material. - GGU collection 319755.

Description. - Semicircular cephalon with stout genal spines that are not in an advanced position. Glabella expands forwards from occipital furrow, with strongly rounded anterior. Separated from anterior border by short (sag.) preglabellar field. Anterior two pairs of glabellar furrows shallow, arcuate, directed backwards. Posterior pair deeper and joined across glabella by shallow furrow. Occipital furrow deepest abaxially, averaging transverse, not connected across axial line. Ocular lobes long (exsag.), terminating approximately at the level of SO. No apparent furrow on ocular lobe. Axial furrows very shallow with glabella defined primarily by change in exoskeletal slope. Interocular cheeks narrow (tr.), maximum width about half basal glabellar width. Wide and gently convex (tr.) extraocular cheeks. Anterior and lateral borders narrow, adjacent border furrow shallow. Posterior border sigmoidal in plan view, with genal angle behind posterior margin of occipital ring. Intergenal spines not developed. Sculpture not preserved.

Discussion. – Olenellus sp. B can be distinguished from the other North Greenland olenellids described here by its lack of a parafrontal band and intergenal spines; additionally the genal spines are not advanced. In overall morphology Olenellus sp. B is closest to O. svalbardensis; it differs in a more rapidly expanding and wider (tr.) glabella which anteriorly is broadly rounded. The configuration of the glabellar furrows described above also aids delimitation of Olenellus sp. B from other members of this genus identified from North Greenland. Olenellus sp. B is reminiscent of Elliptocephala Emmons 1844 from the Lower Cambrian of New York State and Canada, as illustrated by Palmer & Repina (1993, fig. 6.7).

Occurrence in North Greenland. – Aftenstjernesø Formation (Figs 4, 5, collection localities 2 and 3), northern Nyeboe Land. Age: Early Cambrian, *Olenellus* Zone.

Order Corynexochida Kobayashi, 1935 Family Dorypygidae Kobayashi, 1935

Synonym. – Ogygopsididae Rasetti, 1951 (after Palmer in Palmer & Halley 1979).

Remarks. – In proposing the Ogygopsididae, Rasetti (1951) stressed differences in hypostomal structure as one of the reasons for naming a new monotypic family. Palmer (in Palmer & Halley 1979: 81) argued that the hypostomal structure among closely related genera seems to be variable. In addition, he pointed out that Early Cambrian species of *Ogygopsis* have a small number of pygidial segments, approaching those of typical Dorypygidae. Palmer (in Palmer & Halley 1979) also proposed that the nearly isopygous condition of *Ogygopsis* and a thorax with only eight segments were reasons not for distinguishing *Ogygopsis* at the family level, but rather for including it in the Dorypygidae, the course followed here.

Semashko (1969) described *Guraspis*, with type species *G. punktatus*, from the lower Middle Cambrian of the Batenevsky Mountain range, Siberia, USSR. He characterised the genus in terms of its small sagittal length (2.0 - 2.5 mm). Three cranidia illustrated by Semashko (1969, pl.1, figs 8-10) are morphologically similar to specimens of *Ogygopsis virgata* (Romanenko in Romanenko & Romanenko 1962) of equivalent size (Fig. 47.3, 4). It is noted that the immature cranidia of most dorypygid trilobites are of a rather similar morphology and, in the absence of mature cranidia and associated pygidia, it is not known of which dorypygid genus '*Guraspis*' is the immature form.

Genus Ogygopsis Walcott, 1889

Synonym. – Taxioura Resser, 1939 (after Rasetti 1951).

Type species. – By original designation; *Ogygia klotzi* Röminger, 1887, p. 12, pl. 1, fig. 1.

Remarks. – An intriguing aspect of the stratigraphic distribution of *Ogygopsis*, according to Nelson (1963: 247), is its sporadic stratigraphical occurrence. The genus extends from the upper Lower Cambrian through to the medial Middle Cambrian but its stratigraphic distribution is frequently intermittent. Lochman-Balk & Wilson (1958: 322) suggested that this observation may be explained by a series of incursions of extracratonic euxinic biofacies, carrying a long-lived exotic generic stock (*Ogygopsis*), into the "normal" biofacies realms. A slightly different explanation of facies control was suggested by Campbell & Palmer (1976; see also Palmer & Taylor 1976) who noted that the number of individuals, as well as number of species, is high at interfaces between two types of habitat.

Blaker (1986) reported that the fauna of the lower beds of a section through the Henson Gletscher Formation in Freuchen Land (Fig. 5, locality 1) is dominated by species of *Ogygopsis*. The persistence and abundance of *Ogygopsis* through this succession is significant since it is the only documented section in which the stratigraphical distribution of *Ogygopsis* is not sporadic. As a consequence, some of the relationships between different species of *Ogygopsis* are now more evident.

A particular problem concerns the relationship between *Ogygopsis* and *Kootenia* Walcott, 1889. Fritz (1972) attempted to establish a distinction, but detailed discussion following the description of *Ogygopsis virgata* (Romanenko in Romanenko & Romanenko, 1962), below, highlights the difficulties without being able to offer a general solution.

Ogygopsis batis (Walcott, 1916)

Figs 39; 40; 41.2, 3; 42.3, 4, 6, 10

- 1916 Bathyuriscus batis Walcott, p. 337, pl. 48, figs 4,4a.
- 1964 Ogygopsis batis (Walcott); Palmer, p. F7, pl. 2, figs 1-6.
- 1971 Ogygopsis siberica (Romanenko, 1960); Chernysheva, p. 118, pl. 9, figs 1-4.
- 1976 Ogygopsis batis (Walcott, 1916); Egorova et al., p. 94, pl.
- 21, fig. 15 (non pl. 16, fig. 16).
- 1986 Ogygopsis sp. nov. 1; Blaker, p. 66.



Fig. 39. *Ogygopsis batis* (Walcott, 1916). Henson Gletscher Formation. 1, complete specimen, meraspid degree 5, latex of external mould, dorsal view, MGUH 23290 from GGU collection 315093, x 9. 2, complete specimen, meraspid degree 7, dorsal view, MGUH 23292 from GGU collection 301336, x 3. 3, complete specimen, meraspid degree 7, latex of external mould, dorsal view, MGUH 23291 from GGU collection 315093, x 5.5. 4, complete specimen, holaspid, dorsal view, MGUH 23298 from GGU collection 301336, x 3. 6, complete specimen, holaspid, latex of external mould, dorsal view, MGUH 23298 from GGU collection 301336, x 4. 6, cranidium, partially exfoliated, dorsal view, MGUH 23307 from GGU collection 315093, x 8.


Fig. 40. *Ogygopsis batis* (Walcott, 1916). Henson Gletscher Formation. 1, complete specimen; holaspid, latex of external mould, dorsal view, MGUH 23302 from GGU collection 298539, x 3. 2, complete specimen, meraspid degree 7, dorsal view, MGUH 23294 from GGU collection 301336, x 3.5. 3, complete specimen, holaspid, latex of external mould, dorsal view, MGUH 23301 from GGU collection 301336, x 3. 4, damaged complete specimen, holaspid, dorsal view, MGUH 23296 from GGU collection 301336, x 5. 5, damaged complete specimen, holaspid, dorsal view, MGUH 23299 from GGU collection 301336, x 5. 5, damaged cranidium, dorsal view, MGUH 23299 from GGU collection 301336, x 3.5. 6, damaged cranidium, dorsal view, MGUH 23299 from GGU collection 301336, x 3.5. 6, damaged cranidium, dorsal view, MGUH 23299 from GGU collection 301336, x 3.5. 6, damaged cranidium, dorsal view, MGUH 2300 from GGU collection 315093, x 9.

Type material. – As discussed by Palmer (1964), the type material of *Ogygopsis batis* consists of poorly-preserved, slightly metamorphosed specimens from Lower Cambrian strata at Miller Mountain, Nevada, U. S. A. The type series is USNM 62652-62653, Natural History Museum, Smithsonian Institution, Washington D. C.

Figured material. – Complete specimens; MGUH 23290-23291 from GGU collection 315093, MGUH 23292-23301, 23306 from GGU collection 301336, MGUH 23302 from GGU collection 298539. Cranidium; MGUH 23303, 23307 from GGU collection 315093. Hypostome; MGUH 23304 from GGU collec-

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tion 315093. Free Cheek; MGUH 23305 from GGU collection 315093.

Other material. – GGU collections 271748, 271752, 298537, 298539, 298545, 298547, 301336, 301342, 301343, 301351, 315088 (abundant), 315090 (abundant), 315093 (abundant), 315097.

Diagnosis. – Cranidium with prominent glabella reaching to anterior border furrow. Glabellar sides bowed moderately to strongly outwards. Anterior border undeflected by anterior of glabella. Narrow (tr.) palpebral areas. Semicircular pygidium with axis of seven rings, pleural fields crossed by six pairs of pleural furrows.



Fig. 41. Lower Cambrian trilobites.

1. Oryctocephalid genus and species undetermined A. Aftenstjernesø Formation. Partial thorax. dorsal view, MGUH 23514 from GGU collection 313098, x 3.

2, 3. *Ogygopsis batis* (Walcott, 1916). Henson Gletscher Formation. 2, damaged complete specimen; holaspid, dorsal view, MGUH 23297 from GGU collection 301336, x 3. 3, damaged complete specimen, holaspid, dorsal view, MGUH 23300 from GGU collection 301336, x 3.

Border with single, anterolateral pair of spines (Fig. 40.5).

Description. – Prominent glabella, highly convex (tr. & sag.), anterior moderately rounded, reaching to anterior border furrow. Glabellar furrows not apparent, though three pairs of muscle scars evident on some specimens (Fig. 40.1, 4). Occipital furrow straight or gently concave posteriorly, deepest abaxially with marked shallowing axially. Moderately convex (tr.) occipital ring with sagit-tal length approximately one-sixth that of glabella. Posterior margin of occipital ring moderately curved with medial node or short spine. Axial furrow narrow (tr.) and of moderate depth. Palpebral areas gently convex (tr.). Transverse width approximately one-third basal glabellar width. Palpebral lobes gently arcuate, defined by furrow of variable width and depth. Exsagittal length about one-quarter sagittal glabellar length, and centred at glabellar

midlength. Low ocular ridges defined by very shallow furrows. Preocular area of fixed cheek descends rapidly to anterior border furrow. Narrow (sag.), gently convex anterior border with moderately curved anterior margin. Border furrow narrow (exsag.), deepest anteriorly of glabella. Posterior border furrow wide and of moderate depth, slightly shallowing adaxially. Course of anterior section of facial suture gently convex until anterior border furrow then turned adaxially over anterior border with overall slight divergence. Course of posterior sections gently curved and strongly divergent. Free cheek with very gently convex (tr.) ocular platform. Narrow (tr.) convex lateral border, gently curved and increasing in width anteriorly. Border furrow narrow (tr.), shallowing posteriorly. Genal spine stout, of moderate length and directed posteriorly. Posterior border very short (tr.) and narrow (exsag.).

Hypostome subrectangular in outline, moderately con-

Fig. 42. Trilobites from the Henson Gletscher Formation.

5. Zacanthopsis? sp. A. Damaged pygidium, partially exfoliated, dorsal view, MGUH 23463 from GGU collection 298547, x 10.

^{1, 7.} *Kootenia* sp. A. 1a, b, pygidium, partially exfoliated, dorsal and lateral views, MGUH 23445, x 3. 7, damaged pygidium, partially exfoliated, dorsal view, MGUH 23444, x 3. Both from GGU collection 271428.

^{2, 8, 9.} Olenoides sp. A.

^{2,} damaged pygidium, dorsal view, MGUH 23349 from GGU collection 301343, x 16. 8, damaged pygidium, partially exfoliated, dorsal view, MGUH 23350 from GGU collection 298547, x 9. 9, damaged pygidium, partially exfoliated, dorsal view, MGUH 23351 from GGU collection 298547, x 5.

^{3, 4, 6, 10.} *Ogygopsis batis* (Walcott, 1916). 3, free cheek, dorsal view, MGUH 23305 from GGU collection 315093, x 6. 4, damaged hypostome, ventral view, MGUH 23304 from GGU collection 315093, x 13. 6, damaged complete specimen, holaspid, dorsal view, MGUH 23295 from GGU collection 301336, x 6.5. 10, damaged complete specimen, holaspid, dorsal view, MGUH 23306 from GGU collection 301336, x 3.5.

vex transversely, gently convex longitudinally, with pronounced maculae. Posterior lobe of middle body separated by shallow transverse furrow, gently convex (tr. & sag.) and below level of anterior lobe. Border furrow narrow and of moderate depth along posterior border, deepening posterolaterally but more weakly-impressed around anterior of middle body. Posterior border narrow (sag.) and straight, gently convex, without spines. Lateral border narrow, and anterior wings short (tr.).

Holaspid thorax of eight segments, none macropleural.



Gradual widening over anterior three, posterior five of similar width. Axial furrow narrow, transverse width of ring approximately three-tenths that of segment. All rings with median nodes. Pleurae straight, transverse, horizontal over adaxial two-thirds, distally downturned. Pleural furrow wide (exsag.), shallow adaxially, and of moderate depth distally. Anterior pleural band widens distally and extends into short, slender, posterolaterally-directed spine.

Semicircular pygidium gently convex (tr. & sag.). Axis tapers gradually backwards and usually reaches to inner margin of border, or is joined to it by low medial ridge, rarely isolated from border. When isolated a prominent ridge parallels the posterior of the axis and also extends laterally adjacent to axial furrows (Fig. 39.4); forwards extension as far as the posterior of the second axial ring is the maximum observed. Axis formed of seven rings of variable definition and terminal piece. Axial nodes on at most the anterior four rings, although may be absent. Axial furrow narrow (tr.) and shallowing posteriorly. Gently convex pleural fields crossed by five or six pairs of pleural furrows that reach to border furrow. Pleural furrows wide and very shallow, frequently absent. Gently convex, narrow border with median indentation for some specimens. Border with single pair of tiny anterolateral spines; border undulose posteriorly of spine. Border furrow shallow and of variable width.

Sculpture consists of parallel terrace ridges on anterior border of cranidium, lateral border and genal spine of free cheek, anterior wings and border of hypostome and pygidial border. All other parts of exoskeleton with reticulate sculpture of narrow, low ridges.

Ontogeny. – Moulting was presumably a common occurrence during trilobite life histories (Speyer 1985). Little direct evidence of such behaviour is preserved in the Palaeozoic fossil record, however, and this is particularly so for Early Cambrian forms. A poorly represented ontogenetic sequence of late meraspids and holaspids has been recognised for *Ogygopsis batis*. The earliest meraspid stage recognised here for *O. batis* is degree 5 and this single specimen (Fig. 39.1) displays a holaspid-type morphology for both cranidium and pygidium.

No specimens of degree 6 have been identified, whilst specimens of degree 7, the final meraspid stage, have sagittal lengths that range from 8.6 to 18.9 mm. The relatively large size which this species attains whilst still in the meraspid stage is an important aspect of its growth since the maximum length of the meraspid stage is large, in comparison with other genera. It is normally only trilobites that attain considerable final lengths that have large meraspid growth stages. For the material from North Greenland the maximum length of a holaspid of *O. batis* is 49 mm. *Paradoxides* Brongniart, 1822, which is known to grow up to 400 mm, has a maximum meraspid length of only 14 mm (Whittington 1957).

Several of the holaspid specimens have sagittal lengths that are less than the maximum observed for a meraspid

specimen. As was stressed by Alberch *et al.* (1979), growth involves both changes of morphology and size, and these functions do not always have to progress in unison. In trilobite growth, and indeed growth of other arthropods, size increase is a discontinuous process, whereas morphological development will, on the whole, be continuous. For the populations of *Ogygopsis batis* from North Greenland it could be speculated that some members of the population were undergoing greater size increases at each moult, whilst morphological development remained about constant. Substantiation of this theory, however, requires access to large numbers of individual meraspid stages. Alternatively, paedomorphosis by neotony may have occurred within the populations.

Discussion. - In a discussion of the faunas from the Henson Gletscher Formation in southern Freuchen Land (collection locality 1, see Figures 12 and 16) by Blaker (1986: 66), the specimens that are herein referred to as Ogygopsis batis (Walcott, 1916) were described as being representative of two new species of Ogygopsis. The two species were collected from two separate horizons and were thought to be closely related. Subsequent collections from stratigraphically intermediate horizons enabled a revision of the opinion expressed by Blaker (1986). The stratigraphically intermediate specimens show gradual change in morphology through time, and it is now considered that only a single, variable species is represented. Furthermore, the assignment of specimens from stratigraphically higher beds in this section (Fauna 4 in Blaker 1986) to Ogygopsis batis is now considered to be incorrect; these specimens are herein identified as Ogygopsis typicalis (Resser, 1939).

The populations contain many articulated specimens that frequently lack the free cheeks or which have the free cheeks in very close proximity to the specimen. McNamara & Rudkin (1984: 154), noted that it is most common for the free cheeks to be absent from exuviae. Exuviation in the type species of *Ogygopsis*, *O. klotzi* (Röminger, 1887), was described by McNamara & Rudkin (1984: 164) in two specimens with inverted and rotated free cheeks, the cheeks lying in exactly the same position, which were considered to represent the true ecdysial configuration. It was noted, however, that exuviae of *O. klotzi* more commonly occur as exoskeletons lacking only the free cheeks, which is the observed situation in the majority of articulated specimens of *O. batis* from Freuchen Land.

Specimens of *Ogygopsis batis* from the Henson Gletscher Formation which have complete exoskeletons do not have their free cheeks displaced by the same method of ecdysis. None of the free cheeks are inverted but rather they have undergone slight backward displacement and rotation, such that the anterior part of the free cheek has come to rest directly beneath the palpebral area (Fig. 39.4; Fig. 40.3).

Ogygopsis batis is recorded from the latest Toyonian *Anabaraspis splendens* Zone of Siberia by Rozanov *et al.* (1992).

Occurrence in North Greenland. – Henson Gletscher Formation, collection localities 1 and 6 (see Figs 5, 10, 11). Age: Early Cambrian, *Olenellus* Zone.

Ogygopsis typicalis (Resser, 1939)

Figs 43; 44

- 1939 Taxioura typicalis, n. sp., Resser, p. 62, pl. 14, figs 6-14.
- 1939 Taxioura magna, n. sp., Resser, p. 63, pl. 14, figs 1-2 (non 3-5).
- 1944 *Taxioura typicalis* Resser, 1939; Shimer & Shrock, pl. 259, figs 23, 24.
- 1950 *Taxioura elongata* McLaughlin & Enbysk, n. sp, p. 470, pl. 65, figs 2, 9.
- ?1968 Ogygyopsis sp. indet., Fritz, p. 201, pl. 40, fig. 30.
- 1979 Ogygopsis typicalis (Resser); Palmer in Palmer & Halley, p. 82, pl. 12, figs 1-4.

1986 Ogygopsis batis (Walcott, 1916); Blaker, p. 69.

1986 Ogygopsis typicalis (Resser, 1939); Blaker, p. 72.

Type material. – Type series USNM 98565a-g, Natural History Museum, Smithsonian Institution, Washington

D. C. From Middle Cambrian strata of the northern Wasatch Mountains, Idaho, U. S. A.

Figured material. – Cranidium; MGUH 23308 from GGU collection 271750. Free cheek; MGUH 23309 from GGU collection 271750. Hypostome; MGUH 23310-23311 from GGU collection 271750. Pygidium; MGUH 23312-23315 from GGU collection 301346, MGUH 23316-23318 from GGU collection 301342, MGUH 23319 from GGU collection 298547.

Other material. - GGU collections 225706, 271750, 301346.

Diagnosis. – Cranidium subtrapezoidal with long, narrow glabella. Glabellar sides bowed shallowly to moderately outwards. Palpebral area about half (tr.) basal glabellar width. Pygidium with axis of eight rings, pleural fields crossed by seven or more pairs of pleural furrows. Border with one or two pairs of anterolateral spines.

Description. – Cranidium, free cheek and hypostome conform to the description of this species given by Palmer (in Palmer & Halley 1979).

Pygidium gently to moderately convex (tr. & sag.) with slender axis that tapers posteriorly reaching nearly



Fig. 43. *Ogygopsis typicalis* (Resser, 1939). Henson Gletscher Formation. 1, pygidium, dorsal view, MGUH 23314 from GGU collection 301346, x 2. 2, pygidium, dorsal view, MGUH 23315 from GGU collection 301346, x 1.5. 3, free cheek, latex of external mould, dorsal view, MGUH 23309 from GGU collection 271750, x 4. 4a, b, pygidium, dorsal and lateral views, MGUH 23312 from GGU collection 301346, x 2 (see also Fig. 44.1). 5, damaged pygidium, dorsal view, MGUH 23313 from GGU collection 301346, x 1.5.



Fig. 44. *Ogygopsis typicalis* (Resser, 1939). Henson Gletscher Formation. 1. Pygidium, posterior oblique view, MGUH 23312 from GGU collection 301346, x 2 (see also Fig. 43.4). 2a, b, pygidium, partially exfoliated, dorsal and lateral views, MGUH 23318 from GGU collection 301342, x 3. 3, pygidium, partially exfoliated, dorsal view, MGUH 23317 from GGU collection 301342, x 2.5. 4, pygidium, partially exfoliated, dorsal view, MGUH 23316 from GGU collection 301342, x 2.5. h, postome, ventral view, MGUH 23316 from GGU collection 271750, x 3. 6, damaged cranidium, dorsal view, MGUH 23308 from GGU collection 271750, x 2.5. 7, hypostome, latex of external mould, ventral view, MGUH 23310 from GGU collection 271750, x 4.5. 8, pygidium, partially exfoliated, dorsal view, MGUH 23319 from GGU collection 271750, x 4.5. 8, pygidium, partially exfoliated, dorsal view, MGUH 23319 from GGU collection 271750, x 4.5. 8, pygidium, partially exfoliated, dorsal view, MGUH 23319 from GGU collection 271750, x 4.5. 8, pygidium, partially exfoliated, dorsal view, MGUH 23319 from GGU collection 271750, x 4.5. 8, pygidium, partially exfoliated, dorsal view, MGUH 23319 from GGU collection 271750, x 1.5.

to the inner edge of the border. Posterior of axis connected to border by short (sag.) narrow (tr.) ridge. Anterior width of axis variable between one-fifth and one-quarter anterior pygidial width. Axial furrow narrow, shallowing posteriorly. Axis formed of eight well-defined rings, with an incipient ninth on some specimens. Axial rings without median nodes. Inter-ring furrows vary from straight and transverse through to exhibiting a posterior sagittal deflection. Pleural fields gently to moderately convex (tr.), crossed by seven, or more rarely eight, gently curved pleural furrows. Furrows are wide and shallow, just reaching to inner edge of border. Interpleural furrows barely apparent except distally. Narrow border gently convex with median indentation. Border defined by furrow of variable depth which is in places only just discernible. Border with at least a single pair of short and slender anterolateral spines, frequently a second pair is also developed. Posteriorly the border is gently undulose with slight swellings marking the position of incipient spines (Fig. 40.8).

Sculpture of all parts of the pygidium consists of narrow, low, anastomosing terrace ridges which on the axis have a subconcentric arrangement.

Discussion. – Ogygopsis typicalis was first described by Resser (1939) from the basal limestones of the Langston Formation in north-eastern Utah and south-eastern Idaho as part of the so-called *Ptarmigania* fauna. Subsequently, Maxey (1958) designated the fossiliferous unit as the Naomi Peak Limestone Member, since Resser (1939) had not adequately defined the formation or a type locality. Maxey (1958) considered that the age of the Naomi Peak Limestone Member is undoubtedly Middle Cambrian and *O. typicalis* has previously been taken to be characteristic of the early Middle Cambrian (*Albertella* Zone). The recognition of *O. typicalis* in strata of Early Cambrian age from Northern Greenland thus extends the known stratigraphical range of the species significantly.

Recognition of *O. typicalis* in Lower Cambrian strata is also significant because Palmer (1964: F6), in a detailed review of the genus, concluded that the number of pygidial pleural furrows is a character of stratigraphic value. He stated that no Lower Cambrian specimens of *Ogygopsis* have more than six pairs, and all Middle Cambrian specimens have at least seven pleural furrows. The observation is often, but not invariably, correct, making it an unreliable stratigraphical indicator.

Palmer (1964: F7) suggested that Ogygopsis elongata (McLaughlin & Enbysk, 1950) may be a synonym of O. typicalis. Discrimination of the two species was based only on differences in proportion which Palmer thought to be unfounded because the type material of O. elongata is distorted. The holotype of O. elongata is held at the Department of Geology, Washington State University, U. S. A., but unfortunately the paratype material has been lost (together with several other specimens of McLaughlin & Enbysk 1950). It is concluded that O. typicalis and O. elongata (from the Middle Cambrian Metaline Limestone of Pend Oreille County, Washington) are conspecific, following study of the type material of both species.



Fig. 45. *Ogygopsis virgata* (Romanenko, 1962). Henson Gletscher Formation. 1, hypostome, partially exfoliated, ventral view, MGUH 23333 from GGU collection 301343, x 11. 2, pygidium, partially exfoliated, dorsal view, MGUH 23340 from GGU collection 298544, x 12. 3, damaged pygidium, dorsal view, MGUH 23339 from GGU collection 298544, x 4. 4, pygidium, dorsal view, MGUH 23342 from GGU collection 315097, x 5. 5, damaged pygidium, dorsal view, MGUH 23346 from GGU collection 301343, x 3.5. 6, damaged cranidium; dorsal view, MGUH 23321 from GGU collection 315097, x 7.5. 7a, b, pygidium, partially exfoliated, dorsal and lateral views, MGUH 23348 from GGU collection 301343, x 6.

Occurrence in North Greenland. – Henson Gletscher Formation, collection localities 1 and 6 (see Figs 8A, 10, 11). Age: Early Cambrian, *Olenellus* Zone.

Ogygopsis virgata (Romanenko *in* Romanenko & Romanenko, 1962)

Figs 45-48

1962 Kootenia virgata Romanenko in Romanenko & Romanenko, p. 19, pl. 1, figs 9-11.

1968 Ogygopsis antiqua n. sp., Palmer, p. B50, pl. 3, figs 3, 4.

- 1971 Ogygopsis virgata (Romanenko, 1962); Chernysheva, p. 118, pl. 9, figs 5-11.
- ?1975 Ogygopsis batisformis Repina, sp. nov., in Repina et al., p. 145, pl. 22, figs 1-3.
- 1984 Kootenia cf. K. anabarensis Lermontova; Palmer in Dutro et al., p. 1367, figs 2A-F.
- 1986 Ogygopsis antiqua Palmer, 1968; Blaker, p. 66.

Type material. – Information on the type series of *Ogygopsis virgata* has not been traced within the literature. Assignment of specimens from North Greenland to this species is based on comparisons with material described by Chernysheva (1971).



Fig. 46. *Ogygopsis virgata* (Romanenko, 1962). Henson Gletscher Formation. 1, pygidium, latex of external mould, MGUH 23346 from GGU collection 301343, x 3. 2a, b, damaged pygidium, partially exfoliated, dorsal and lateral views, MGUH 23343 from GGU collection 315097, x 3. 3, cranidium, dorsal view, MGUH 23327 from GGU collection 298544, x 7. 4, damaged thoracic segment, dorsal view, MGUH 23337 from GGU collection 315097, x 6. 5, hypostome, ventral view, MGUH 23332 from GGU collection 301343, x 4. 6a, b, pygidium, partially exfoliated, dorsal and lateral views, MGUH 23347 from GGU collection 301343, x 5. 7, hypostome, ventral view, MGUH 23335 from GGU collection 315097, x 5.5.



Fig. 47. *Ogygopsis virgata* (Romanenko, 1962). Henson Gletscher Formation. 1a, b, cranidium, dorsal and lateral views, MGUH 23325 from GGU collection 298544, x 5.25. 2, pygidium, partially exfoliated, dorsal view, MGUH 23341 from GGU collection 298544, x 8.5. 3, damaged meraspid cranidium, dorsal view, MGUH 23323 from GGU collection 315097, x 25. 4, meraspid cranidium, dorsal view, MGUH 23324 from GGU collection 298544, x 6.

Figured material. – Cranidium; MGUH 23320-23323 from GGU collection 315097, MGUH 23324-23327 from GGU collection 298544, MGUH 23328 from GGU collection 301343. Free cheek; MGUH 23329 from GGU collection 298544, MGUH 23330 from GGU collection 315097. Hypostome; MGUH 23331-23333 from GGU collection 301343, MGUH 23334 from GGU collection 298544, MGUH 23335-23336 from GGU collection 315097. Thoracic segment; MGUH 23337 from GGU 315097. Pygidium; MGUH 23338-23341 from GGU 298544, MGUH 23342-23344 from GGU 315097, MGUH 23345-23348 from GGU 301343.

Other material. – GGU collections 298544, 301343 (abundant), 315097 (abundant).

Diagnosis. – Glabella elongate, without furrows, the gently curved anterior reaching anterior border furrow. Pygidia semicircular, with six or seven rings in the axis. Border with 4 or 5, but varying from 2 to 7, pairs of spines.

Description. – Glabella elongate and of moderate convexity (tr. & sag.); sides convex with about equal convergence backwards and forwards of midlength; slight contraction at junction with ocular ridge. Glabellar anterior gently curved, reaching anterior border furrow. Glabellar furrows not developed, although 3 pairs of diffuse muscle scars apparent on some cranidia (Fig. 46.3). Occipital furrow gently curved posteriorly, deepest abaxially, shal-

median node on posterior margin. Sagittal length of occipital ring approximately one-seventh that of glabella. Glabella laterally defined by narrow (tr.) furrows. Gently convex (tr.) palpebral areas slope gently downwards from axial furrow; transverse width approximately two-thirds that of glabella across SO. Palpebral lobes very gently curved, centred slightly posteriorly of glabellar midlength. Lobes defined by narrow (tr.) furrow; exsagittal length of lobes about one-quarter sagittal glabellar length. Low ocular ridges defined by shallow furrows or change in exoskeletal slope. Preocular cheek descends steeply to the anterior border furrow. Convex anterior border narrowest in front of glabella with gradual widening abaxially. Defined distally by narrow furrow that deepens and widens in front of glabella. Posterior border narrow adaxially, increasing in width distally, widest at fulcrum. Border horizontal over adaxial half to point of geniculation, moderately downturned distally. Close to axial furrow posterior border furrow wide and shallow, increasing in depth and width abaxially. Short anterior section of facial suture very slightly convex, variable from parallel to convergent. Posterior sections very strongly divergent and gently curved.

lowing adaxially. Occipital ring moderately convex (tr.),

in lateral profile horizontal, or directed gently upwards,

Free cheek with narrow (tr.) ocular platform. Lateral border of moderate width (tr.), defined anteriorly by shallow furrow, poorly defined posteriorly. Border widens posterolaterally and is continuous with a long, slender genal spine. Exsagittal length of spine slightly less than



Fig. 48. *Ogygopsis virgata* (Romanenko, 1962). Henson Gletscher Formation. 1, damaged free cheek, dorsal view, MGUH 23329 from GGU collection 298544, x 5.5. 2, pygidium, dorsal view, MGUH 23338 from GGU collection 298544, x 5.5. 3, damaged hypostome, ventral view, MGUH 23331 from GGU collection 301343, x 3.5. 4, damaged cranidium, dorsal view, MGUH 23328 from GGU collection 301343, x 3.5, cranidium, partially exfoliated, dorsal view, MGUH 23326 from GGU collection 298544, x 5. 6, free cheek, dorsal view, MGUH 23330 from GGU collection 315097, x 2.5. 7, damaged cranidium, dorsal view, MGUH 23320 from GGU collection 315097, x 6. 8, pygidium, dorsal view, MGUH 23344 from GGU collection 315097, x 6. 9, hypostome, ventral view, MGUH 23334 from GGU collection 298544, x 7.25. 10, hypostome, ventral view, MGUH 23336 from GGU collection 315097, x 6.5. 11, damaged pygidium, dorsal view, MGUH 23345 from GGU collection 301343, x 2.25.

that of lateral border. Posterior border very short (tr.) and ill-defined.

Hypostome strongly convex (tr. & sag.), subrectangular in outline. Elongate middle body divided by shallow, transverse furrow into anterior and posterior lobes; furrow only defined laterally. Sagittal length of anterior lobe between four and five times that of posterior. Very strongly developed maculae on posterior margin of anterior lobe. Posterior lobe slopes strongly down to posterior border furrow. Posterior border narrow and gently curved. Lateral border widens anteriorly with distinct flaring at level of maculae, and bears three pairs of small, stout spines. Lateral border defined anterolaterally by deep and wide (tr.) furrow that shallows rapidly posteriorly. Anterior wings short and blunt.

Thorax known only from disarticulated segments. Axial rings moderately convex (tr.) with prominent articulating half-ring, and median node developed close to the posterior margin of ring. Transverse width of ring approximately one-quarter that of segment. Pleurae with wide (exsag.) furrow that deepens and narrows distally. Pleura horizontal over adaxial three-quarters to fulcrum, downturned distally, extended into slender spine that is directed posterolaterally.

Pygidium semicircular in outline, gently convex (tr. & sag.) with slender axis that tapers gradually backwards. Axis of moderate convexity (tr.) formed of six or seven rings and short (sag.) terminal piece. Inter-ring furrows straight to gently concave posteriorly, of moderate depth. Axial nodes of variable development; from weak but evident on all rings, to absent. Axis reaches to inner edge of posterior border, or is joined to it by a short postaxial ridge. Axial furrow narrow and shallowing posteriorly, with the posterior of the axis defined by a change in slope. Some specimens possess a conspicuous ridge around the posterior of the axis (Fig. 48.11). Very gently convex pleural fields crossed by six pairs of wide pleural furrows. Furrows are of medium depth and reach to the border furrow, with the anterior-most pair occasionally being continuous across the border. Narrow pleural furrows evident on at least the anterior few pleurae, rarely on all pleurae, terminate as small depressions in the border furrow. Border furrow wide, variable in depth with parts of the border frequently being poorly-defined. Border widens posteriorly with median indentation of variable development. Morphology of the border spines is extremely wide ranging; minimum development being two pairs of short spines, and undulose outer margin posteriorly of the second pair. A progression is observable within the sample to very undulose margins posteriorly of the second pair of well-developed spines, caused by the emergence of incipient spines. An intermediate morphology is a border that possesses four or five pairs of short border spines, with indications of a further two pairs. The most extreme development is a pygidial border with seven pairs of more-or-less equally spaced, slender spines directed strongly backwards.

Sculpture of the cranidium consists of terrace ridges on

the anterior border with all other parts, except the posterior border, having a prominent meshwork of ridges. On the glabella, and to a lesser extent the fixed cheeks, the ridges have a subconcentric arrangement. Lateral border of free cheek with terrace ridges on the anterior part with the arrangement of ridges becoming less ordered both posteriorly and on the genal spine. Ocular platform with raised network of coarse ridges. The hypostome has the anterior lobe of the middle body and anterior wings sculptured with very coarse, widely-spaced ridges that are roughly subparallel and are aligned longitudinally. For other specimens the ridges form an irregular polygonal network. The posterior lobe lacks sculpture, whilst the lateral and posterior borders have terrace ridges. A subconcentric pattern of coarse ridges occurs on the thoracic axial rings, with anastomosing ridges on the pleurae. A polygonal network of ridges covers all parts of the pygidium.

Discussion. – Cranidia of *Ogygopsis virgata* have a more deeply impressed anterior border furrow than cranidia of *O. typicalis* (compare Fig. 44.6 with Fig. 46.3). Pygidia of *Ogygopsis typicalis* differ in possessing eight well-defined axial rings and an incipient ninth, whereas six or seven rings are present in pygidia of *O. virgata*. While *O. typicalis* may have 1 or 2 pairs of short spines on the pygidial border, up to 4 or 5 pairs of spines are normally present in *O. virgata*, although the extreme is from 2 to 7 pairs.

Studied material of *O. virgata* was collected from a single bed (5-10 cm thick), with the three collections (Fig. 10, GGU 298544, 301343, 315097) having been taken laterally at approximately 20 m intervals in order to determine if population characteristics remain constant. The pygidia in this population pose an intriguing taxonomic problem.

Within the three samples there are specimens which could be referred to the type species of *Kootenia* (*K. dawsoni* Walcott, 1889) because of the numerous pairs of pygidial spines. There is a complete gradation in the number of spines from such specimens to forms which could be placed in species which have been referred to *Ogygopsis*. These have reduced both the number and degree of development of pygidial border spines to the extreme where the pygidial margin is merely undulose. This range of variation is not related to size.

A subjective, arbitrary separation taken on pygidial morphology could place some specimens in *Kootenia* and some in *Ogygopsis*. This is entirely unsatisfactory since the material is considered to represent a single highly variable species. Additionally, the type species of *Ogygopsis*, although it has exceedingly reduced border spines, has more pygidial axial rings (at least 10) than any specimen in the population. This single character alone, however, is not sufficient to discriminate between the genera.

There are specimens in the three samples which resemble many of the large number of described species of

Kootenia, and some of Ogygopsis. It is premature to propose large scale synonomy at specific level without a major revision of the relevant species, many of which are known from very few and incomplete specimens. This problem was addressed by Romanenko in Chernysheva (1971: 117) in a discussion on the generic limits of Ogvgopsis. He concluded that the Siberian species (see below) of 'Kootenia' with seven pairs of border spines form a distinct group that is more characteristic of Ogygopsis. As a consequence, Romanenko added the following species to Ogygopsis; K. anabarensis Lermontova, 1951, K. jakutensis Lermontova, 1951, K. moori Lermontova, 1951 and K. virgata Romanenko in Romanenko & Romanenko 1962. These assignments, except that of O. virgata, were subsequently reversed by Egorova et al. (1976) who concluded that Romanenko's proposals were premature in the absence of a thorough revision of Kootenia.

As stated above, there is unequivocal evidence from the material to hand that a seven-spined form which would be referred by some to Kootenia, and a form with few pairs of border spines, which would be referred to Ogygopsis, are extremes of variation within a single species. To follow Romanenko (in Chernysheva 1971) and place only the seven-spined species of *Kootenia* in *Ogy*gopsis does not solve the taxonomic problem. Furthermore, there is little justification for placing only the seven-spined forms in Ogygopsis, whilst still regarding sixspined and eight-spined forms as species of Kootenia. This is particularly highlighted by the more than fifty described species of Kootenia with six pairs of border spines, with many of these exhibiting considerable intraspecific morphological variation. It has not been possible to delimit any characters by which these species consistently differ from seven-spined forms. Even using the number of pairs of border spines is unreliable. For example, specimens with 6 pairs of pygidial border spines which have been assigned to Kootenia jakutensis Lermontova, 1951 by various Soviet workers (e.g. Suvorova 1964; Savitsky et al. 1972) frequently have a seventh pair of border spines represented by only slight swellings (see Suvorova 1964, pl. 7, figs 11-12). The opinion of Romanenko (in Chernysheva 1971) that only species of Kootenia with seven pairs of pygidial spines should be assigned to Ogygopsis is therefore rejected.

There is little doubt that *Ogygopsis* and *Kootenia* are similar, and the distinctions given by various authors between the two genera are often tenuous. Fritz (1972:

36) attempted to discriminate cranidia of the two genera on the basis that "species of *Ogygopsis* average larger than do those of *Kootenia*. Glabellar sides are either straight and parallel or convex with equal convergence forward and back, and they do not rise as abruptly from the axial furrow as on *Kootenia*". For the pygidia he considered *Ogygopsis* pygidia to be "not so convex as those on *Kootenia*, there are more rings on the axis and more furrows on the pleural field. Most species lack spines on the border, but up to six pairs may be present". The cranidial distinctions proposed are not satisfactory as they vary within the large populations from North Greenland and can also vary due to preservation and size. This is also true of the pygidial characters mentioned (with the exception of the number of axial rings).

The possibility remains that *Kootenia* and *Ogygopsis* should be synonymised, creating a highly variable genus containing highly variable species within which morphological discontinuities upon which to base distinct taxa do not exist or are not yet recognised.

It is only possible here to attempt to synonymise forms of which the type material has been examined. Palmer (1968: B50) described *Ogygopsis antiqua* from the Lower Cambrian Hillard Limestone in the Alaska – Yukon boundary area. Its pygidial axis is formed of six complete rings and an ill-defined seventh, with the border bearing two or three pairs of short border spines. The number of pleural furrows was described as five, but study of the type material suggests that there are in fact six pairs, with the posteriormost pair being positioned adjacent to the axial furrow. The sculpture of these specimens is consistent with that described here in the material from the Henson Gletscher Formation.

Palmer (1964, in Palmer & Halley 1979) mentioned an undescribed Lower Cambrian species of *Ogygopsis* characterised by six or seven pairs of marginal pygidial spines, and five or six well-defined pleural furrows. This material (U.S. Geological Survey Denver collection 3701-CO) is from the upper part of the Harkless Formation in the Paymaster Canyon area of Esmeralda County, Nevada, and has been dated as being of late *Bonnia – Olenellus* Zone age, equivalent to *Olenellus* Zone of current usage (A. R. Palmer, written communication 1985). Specimens in this collection are slightly distorted but examination has not revealed consistent morphological differences from *Ogygopsis virgata* (Romanenko in Romanenko & Romanenko 1962).

Fig. 49. Trilobites from the Henson Gletscher Formation.

^{1, 2, 6, 7.} Dorypygidae genus and species undetermined. 1, pygidium, partially exfoliated, dorsal view, MGUH 23450, x 4. 2, damaged cranidium, partially exfoliated, dorsal view, MGUH 23448, x 6. 6, damaged pygidium, partially exfoliated, dorsal view, MGUH 23449, x 8.5. 7, damaged cranidium, partially exfoliated, dorsal view, MGUH 23447, x 7. All from GGU collection 301340. 3, 9. *Kootenia oscari* sp. nov. 3, paratype, damaged pygidium, partially exfoliated, dorsal view, MGUH 23410, x 4. 9, paratype, damaged pygidium, partially exfoliated, dorsal view, MGUH 23408, x 5. Both from GGU collection 301342.

^{4,} Olenoides sp. C, damaged pygidium, partially exfoliated, dorsal view, MGUH 23355 from GGU collection 301343, x 3.

^{5, 8.} Olenoides sp. B.

^{5,} damaged pygidium, partially exfoliated, dorsal view, MGUH 23353 from GGU collection 298544, x 15. 8, pygidium, partially exfoliated, dorsal view, MGUH 23354 from GGU collection 298547, x 6.5.

^{10,} Olenoides sp. A, damaged pygidium, partially exfoliated, dorsal view, MGUH 23352 from GGU collection 298544, x 2.5.



An early Middle Cambrian fauna described by Palmer (in Dutro *et al.* 1984) from the Doonerak anticlinorium, central Brooks Range, Alaska, includes specimens assigned to *Kootenia* cf. *K. anabarensis*. In pygidial morphology they are identical to the *Kootenia*-type end member of the Greenland populations, whilst cranidial morphology is also similar. This material is also considered to be conspecific with *Ogygopsis virgata* (Romanenko in Romanenko & Romanenko 1962).

Occurrence in North Greenland. – Henson Gletscher Formation, collection locality 1 (see Figs 8A, 10). Age: Early Cambrian, *Olenellus* Zone.

Genus Olenoides Meek, 1877

Synonyms. – *Neolenus* Matthew, 1899 (after Palmer 1954), *Kootenia (Duyunia)* Chien, 1961 (after Suvorova 1964), *Kootenina* Fedyanina, 1962 (after Suvorova 1964).

Olenoides sp. A

Figs 42.2, 8, 9; 49.10

Figured material. – Pygidium; MGUH 23349 from GGU 301343, MGUH 23350-23351 from GGU 298547, MGUH 23352 from GGU 298544.

Description. - Gently convex (tr. & sag.), semicircular pygidium with posteriorly tapering axis joined to inner margin of border. Axis of four well-defined rings, ill-defined fifth and terminal piece. Inter-ring furrows very gently concave posteriorly, axis laterally defined by narrow (tr.) furrows. Axial nodes may be developed on anterior two or three rings. Pleural fields crossed by four pairs of wide pleural furrows that terminate in pits in border furrow. Narrow pleural furrows, shallower than pleural, weakly sigmoidal in outline, also terminate in pits in border furrow. Gently convex, poorly-defined border bearing five pairs of spines. Anterior four pairs of about equal spacing apart; distance between fourth and fifth considerably reduced. All except the fifth pair of spines are long, slender, directed backwards and confluent with the corresponding anterior pleural band. Fifth pair very short, slender and positioned almost immediately behind axial furrows. Sculpture of the border is of closely-spaced medium granules, with low granules on axis and pleural fields.

Discussion. – The number of species, from both Lower and Middle Cambrian strata, assigned to *Olenoides* is considerable. The majority of these species have been based on small populations and, as such, ranges of intraspecific variation are unknown. This is particularly relevant since it is the pygidium of *Olenoides* that is most diagnostic. As the present species is known from only four pygidia, identification at the specific level, or comparison of the specimens to described species, has not been made.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, collection locality, 1). Age: Early Cambrian, *Olenellus* Zone.

Olenoides sp. B

Fig. 49.5, 8

Figured material. – Pygidium; MGUH 23353 from GGU collection 298544, MGUH 23354 from GGU collection 298547.

Remarks. – This differs from *Olenoides* sp. A in having five well-defined axial rings and an ill-defined border with four pairs of spines. Border spines are long, slender and curved strongly posteriorly with the posterior pair situated some distance from the axial line. Pleural furrows are additionally of greater depth.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, collection locality 1). Age: Early Cambrian, *Olenellus* Zone.

Olenoides sp. C

Fig. 49.4

Figured material. – Pygidium; MGUH 23355 from GGU collection 301343.

Remarks. – This species is characterised by four pairs of border spines and an axis of five rings and a terminal piece. It differs from *Olenoides* sp. B in pygidial outline, which is more quadrate, shallower pleural furrows, a border that is less clearly defined and interpleural furrows that are very wide and shallower. Interpleural furrows are poorly defined.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, collection locality 1). Age: Early Cambrian, *Olenellus* Zone.

Genus Bonnia Walcott, 1916

Type species. - Bathyurus parvulus Billings, 1861.

Bonnia brennus (Walcott, 1916)

Figs 50; 51.1-5, 8, 10

- 1916 Corynexochus brennus Walcott, p. 314, pl. 57, figs 3-3b.
- 1936 Bonnia quebecensis, n. sp., Resser, p. 10 (after Lochman 1947) nom. nud.
- 1948 Bonnia brennoides Rasetti, n. sp., p. 16, pl. 4, figs 1-6.
- 1948 Bonnia similis Rasetti, n. sp., p. 17, pl. 4, figs 7-10.
- 1948 *Bonnia brennus* (Walcott); Rasetti, p. 16, pl. 3, figs 16-25. (Includes complete synonomy).

Type material. – Type series USNM 62748-62750, Natural History Museum, Smithsonian Institution, Washington D. C., from Lower Cambrian conglomerates at Bic, Quebec, Canada.

Figured material. – Cranidium; MGUH 23356-23360 from GGU collection 301346, MGUH 23361-23362 from GGU collection 270563, MGUH 23363-23364 from GGU collection 270579. Pygidium; MGUH 23365-23367 from GGU collection 301346, MGUH 23368 from GGU collection 270579, MGUH 23369-23370 from GGU collection 270563. Free cheek; MGUH 23371 from GGU collection 301346. Hypostome; MGUH 23372-23374 from GGU 301346.

Other material. - GGU collections 218681, 225709, 225712, 298553, 301340, 301346 (abundant), 301349, 315110.

Diagnosis. – Glabella with single pair of weakly-defined furrows and strongly rounded anterior. Posterior border furrow very broad (exsag.) and shallow. Hypostome with lateral border widening slightly at level of maculae and extending into short posterolaterally-directed spine. Anterior wings sharply pointed. Semicircular pygidium with axis of three rings, ill-defined fourth, and terminal piece. Border with slight median indentation and single pair of short anterolateral spines.

Description. – Cranidium with prominent glabella that is strongly convex (tr. & sag.). Moderate expansion of glabella forwards from SO, broadly curved across anterior. Glabella widest slightly posteriorly of adaxial termination of ocular ridges. Single pair (S1) of weakly developed glabellar furrows; shallow and directed gently backwards. On some specimens impressions of three pairs of muscle scars (see Fig. 50.6a). Occipital furrow wide (sag.) and curved gently posteriorly; deepest distally. Occipital ring strongly convex (tr.), sagittal length approximately one-ninth that of glabella. Glabella laterally defined by broad (tr.) furrow of moderate depth with distinct pit posteriorly of adaxial termination of ocular ridge. Palpebral areas gently convex (tr.) and moderately to strongly downsloping in lateral profile. Palpebral lobes

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centred slightly backwards of glabella midpoint; exsagittal length about one-third sagittal glabellar length. Ocular ridges low. Anterior border furrow wide (exsag.) in front of ocular ridges, markedly narrower anteriorly of glabella. Anterior border of moderate width (exsag.), narrowing in front of glabella. Posterior border directed weakly anterolaterally, subtriangular in outline, defined by shallow, broad furrow. Anterior section of facial suture short, convergent in gentle curve forwards from palpebral lobe. Posterior section strongly divergent in gentle curve back to posterior margin. Free cheek with gently convex (tr.) ocular platform and lateral border of moderate width that widens posterolaterally, and is continuous with the genal spine. Posterior border very short (exsag.); genal spine of moderate length and curved gently posteriorly.

Hypostome with long (sag.) middle body, sharply curved anterior margin and bluntly rounded posterior. Middle furrow shallow, transverse and gently concave posteriorly. Posterior border narrow (sag.), gently convex, almost straight. Lateral border widens slightly, with distinct flare extending into small posterolaterally directed spine at level of maculae. Border well- defined by deep furrow, that narrows along the posterior border. Anterior border narrow (sag.), very sharply rounded, defined by shallow furrow. Anterior wings large and strongly pointed.

Pygidium semicircular in outline, gently convex (tr. & sag.) with posterior margin almost straight and bearing slight median indentation. Axis of three well-defined rings, occassionally an ill-defined fourth, and a terminal piece that reaches to the inner edge of the border. Axis gently convex (tr.), tapering slightly backwards over anterior three rings, posteriorly expanded. Pleural fields gently convex (tr.), crossed by three or four pairs of pleural furrows that extend to the border furrow, anterior pair of greatest depth. Interpleural furrows wide (exsag.) and very shallow, absent on some specimens. Gently convex border narrows anterolaterally; defined by wide and shallow furrow that is not continuous around the posterior of the axis. Border with single pair of short, anterolateral spines, posteriorly of which the margin is undulose.

Low terrace ridges form the sculpture of the anterior border of the cranidium, lateral border and genal spine of the fixed cheek and pydidial border. Glabella with concentrically-arranged ridges on anterior that become more irregular posteriorly. Fixed cheeks with irregular arrangement of short ridges and coarse granules. Anterior border of hypostome with coarse terrace ridges which are of lower relief and concentrically- arranged on the middle body.

Discussion. – Rasetti (1948) described a number of Lower Cambrian species of *Bonnia* from limestone conglomerates in the lower St. Lawrence Valley, Quebec, Canada. He considered *Bonnia brennoides* Rasetti, 1948 to be very similar to *B. brennus*, differing only in shallower axial furrows, and an occipital ring of more uniform width and lower elevation. Examination of the type material indicates that such differences are not consis-



Fig. 50. Bonnia brennus (Walcott, 1916). Henson Gletscher Formation, 1, damaged cranidium, partially exfoliated, dorsal view, MGUH 23359 from GGU collection 301346, x 2.1. 2, damaged pygidium, partially exfoliated, dorsal view, MGUH 23367 from GGU collection 301346, x 2.8. 3, free cheek, partially exfoliated, dorsal view, MGUH 23371 from GGU collection 301346, x 1.8. 4a, b, damaged cranidium, partially exfoliated, dorsal and lateral views, MGUH 23358 from GGU collection 301346, x 2.8. 5a, b, pygidium, partially exfol-iated, dorsal and lateral views. MGUH 23365 from GGU collection 301346, x 2.5. 6a, b, damaged cranidium, partially exfoliated, dorsal and lateral views, MGUH 23360 from GGU collection 301346, x 2.5. 7, hypostome, ventral view, MGUH 23372 from GGU collection 301346, x 3.2. 8, hypostome, partially exfoliated, ventral view, MGUH 23374 from GGU collection 301346, x 3.5. 9a, b, cranidium, partially exfoliated, dorsal and lateral views, MGUH 23356 from GGU collection 301346, x 2.5. 10a, b, pygidium, partially exfoliated, dorsal and lateral views. MGUH 23366 from GGU collection 301346, x 2.5. 11, damaged cranidium, partially exfoliated, dorsal view, MGUH 23357 from GGU collection 301346, x 2.1. 12, hypostome, partially exfoliated, ventral view, MGUH 23373 from GGU collection 301346, x 4.9.

tent, and the specimens in any case fall within the range of morphology exhibited by the North Greenland populations of *B. brennus. Bonnia similis* Rasetti, 1948 was also considered by Rasetti to closely resemble *B. brennus*, but several differences in cranidial morphology were cited. The type material of this species also shows no consistent differences from *B. brennus* in the morphology of the cranidium, with the exception of more anteriorly-situated palpebral lobes. According to Rasetti, the cranidium of *B. similis* also differed in entirely lack-

Fig. 51. Trilobites from the Sæterdal Formation. 1-5, 8, 10. Bonnia brennus (Walcott, 1916). 1a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23361 from GGU collection 270563, x 3.2. 2, pygidium, internal mould, dorsal view, MGUH 23368 from GGU collection 270579, x 4.2. 3a, b, pygidium, internal mould, dorsal and lateral views, MGUH 23370 from GGU collection 270563, x 2.8. 4, pygidium, internal mould, dorsal view, MGUH 23369 from GGU collection 270563, x 3.2. 5, cranidium, internal mould, dorsal view, MGUH 23364 from GGU collection 270579, x 2.8 8a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23363 from GGU collection 270579, x 2.8. 10a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23362 from GGU collection 270563, x 2.8. 6, 9, 11, Ptychoparioid genus and species undetermined B. 6, cranidium, internal mould, dorsal view, MGUH 23579 from GGU collection 270563, x 4.5. 9, cranidium, internal mould, dorsal view, MGUH 23580 from GGU collection 270563, x 3.9. 11, cranidium, internal mould, dorsal view, MGUH 23581 from GGU collection 270568, x 2.5.

7, Ptychoparioid genus and species undetermined C. Damaged cranidium, internal mould, dorsal view, MGUH 23582 from GGU collection 270563, x 2.5.



ing surface sculpture. However, two incomplete paratype cranidia that were not figured have a sculpture comparable to that found on specimens of B. brennus from North Greenland. The pygidia of the two species can not be differentiated. Since it is the pygidium that is most diagnostic of *Bonnia* species, it is suggested that specimens with smooth cranidia and slight differences in the position of the palpebral lobe are merely extremes of intraspecific variation within *B. brennus*. The inclusion of *B. quebecensis* in the synonomy of *B. brennus* follows

Lochman (1947). Resser (1936) neither figured nor described *B. quebecensis* in connection with his proposal of the species and it is considered a *nomen nudum*; the type material has not been examined.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, 11, localities 1 and 6). Sæterdal Formation, (Fig. 8B). Age: Early Cambrian, *Olenellus* Zone.

Genus Kootenia Walcott, 1889

Synonyms. – Notasaphus Gregory, 1903, Kootenia (Tienzhuia) Chu, 1960.

Type species. – Bathyuriscus (Kootenia) dawsoni Walcott, 1889, p. 446.

Remarks. – Chu (1960) erected Kootenia (Tienzhuia) with K. (T.) gansuensis as type species. The original figures of this species are very poor, though the specimens were subsequently refigured in Lu *et al.* (1965, pl. 16, figs 20, 21). It is of note that the pygidium is described in the subgeneric diagnosis as having an axis of 6 or 7 rings; this was thought to be an unusually large number for the genus, although it is now known that several of the species from North Greenland have a similar number. There is no reason for maintaining the subgenus, following study of the plates and the subgeneric diagnosis. Indeed, the type specimens are so badly preserved that the type species is probably unrecognisable.

In an appraisal of seven-spined species of *Kootenia* by Palmer in Dutro *et al.* (1984), it was stated that there are 122 known species of *Kootenia*. In fact the number of described species is greater, because this figure does not take into account many of the species recorded from China. Although the genus contains so many described species, many are known from material that is inadequate for purposes of comparison, particularly those described from cranidia alone. Such species are not recognisable since the cranidia of different recognisable species of *Kootenia* are frequently almost identical and species that do not have pygidia assigned to them cannot be diagnosed.

The vast number of species assigned to *Kootenia* has arisen because the majority of new discoveries of *Kootenia* contain material that is considered to be slightly different from described species. Such slight variations between geographically-isolated populations may result from intraspecific variation. Large populations of a single *Kootenia* species are rare, and the amount of variability within species based on few specimens is difficult to assess accurately. Although a thorough revision of the genus is beyond the scope of this study, where applicable, possible synonyms are suggested. Ironically, despite the abundance of available specific names in *Kootenia*, much of the material from North Greenland can not be assigned to any described taxon, and it is unfortunately necessary to erect further species.

Kootenia marcoui (Whitfield, 1884)

Figs 52; 53; 54.1-6, 10, 11; 55.1-9, 11

- 1884 Dikellocephalus? marcoui Whitfield, p. 150, pl. 14, fig. 7.
- 1886 Olenoides marcoui (Whitfield); Walcott, p. 186, pl. 26, figs 5-5b.
- 1890 *Olenoides marcoui* (Whitfield); Walcott, pl. 94, figs 2-2b.
- 1897 Dorypyge marcoui (Whitfield); Matthew, p. 187.
- 1937 Kootenia marcoui (Whitfield); Resser, p. 16.
- 1938 Kootenia browni n. sp., Resser, p. 84, pl. 4, figs 8-11.
- 1938 Kootenia virginiana n. sp., Resser, p. 85, pl. 4, figs 1-7.
- 1938 Kootenia currieri n. sp., Resser, p. 85, pl. 4, figs 33-35.
- 1948 Kootenia cf. marcoui (Whitfield); Rasetti, p. 14, pl. 2, fig. 7.
- 1955 Kootenia marcoui (Whitfield) 1884; Shaw, p. 786, pl. 74, figs 1-4.
- 1986 Kootenia sp. nov.; Blaker, p. 69.

Type material. – Holotype AMNH 236 in the collections of the American Museum of Natural History, New York, from slates of Parker Quarry (USNM locality 319g) about 150 feet above the base of the Parker Slate.

Figured material. - Cranidium; MGUH 23375-23377 from GGU collection 271748, MGUH 23378 from GGU 270564, MGUH 23379 from GGU collection 270590, MGUH 23380 from GGU collection 301342, MGUH 23381-83 from GGU collection 298547. Free check: MGUH 23384-23385 from GGU collection 271748, MGUH 23386 from GGU collection 270563, MGUH 23387 from GGU collection 270564. Hypostome; MGUH 23388 from GGU collection 271748, MGUH 23389 from GGU collection 301342, MGUH 23390-23391 from GGU collection 298547. Thoracic segment; MGUH 23392 from GGU collection 270564. Pygidium; MGUH 23393-23395 from GGU collection 271748, MGUH 23396-23398 from GGU 301342, MGUH 23399-23400 from GGU collection 270590, MGUH 23401-23403 from GGU collection 270564, MGUH 23404-23406 from GGU collection 298547.

Other material. – GGU collections 270564, 270590, 271748 (abundant), 298547, 301342.

Diagnosis. – A species of *Kootenia* with seven pairs of long, slender, pygidial border spines, all of approximate-



Fig. 52. *Kootenia marcoui* (Whitfield, 1884). Henson Gletscher Formation. 1, damaged cranidium, dorsal view, MGUH 23377 from GGU collection 271748, x 3.5. 2, pygidium, partially exfoliated, dorsal view, MGUH 23394 from GGU collection 271748, x 3.25. 3, free cheek, dorsal view, MGUH 23384 from GGU collection 271748, x 2.5. 4, hypostome, ventral view, MGUH 23388 from GGU collection 271748, x 5. 5a, b, cranidium, dorsal and lateral views, MGUH 23376 from GGU collection 271748, x 6. 6, free cheek, partially exfoliated, dorsal view, MGUH 23385 from GGU collection 271748, x 3. 7, cranidium, dorsal view, MGUH 23375 from GGU collection 271748, x 7.5. 8, damaged pygidium, dorsal view, MGUH 23395 from GGU collection 271748, x 3. 9a, b, pygidium, partially exfoliated, dorsal view, MGUH 23398 from GGU collection 301342, x 3.



Fig. 53. *Kootenia marcoui* (Whitfield, 1884). Henson Gletscher Formation. 1a, b, pygidium, partially exfoliated, dorsal and posterior views, MGUH 23405 from GGU collection 298547, x 2.5. 2, damaged hypostome, partially exfoliated, ventral view, MGUH 23390 from GGU collection 301342, x 4. 3, hypostome, partially exfoliated, ventral view, MGUH 23390 from GGU collection 298547, x 4.5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23380 from GGU collection 301342, x 3. 5, hypostome, partially exfoliated, ventral view, MGUH 23391 from GGU collection 298547, x 6.

ly equal length, and rarely an incipient eighth pair of spines. Axis of seven rings. Coarse reticulate sculpture on all parts of pygidium. Maximum development of pygidial axial nodes is on anterior four rings, minimum is on anterior ring only.

Description. - Glabella moderately convex (tr. & sag.), subrectangular in outline with very gently curved anterior; axial furrow deep and narrow; anterior of glabella reaches to anterior border furrow. Faint indications of up to three pairs of glabellar furrows. SO gently concave posteriorly, wide (sag.) and of moderate depth, deepest abaxially. Occipital ring moderately convex (tr.), in lateral profile slopes gently upwards with small median spine on posterior margin. Sagittal length of ring approximately one-seventh that of glabella. Palpebral areas very gently convex (tr.), transverse width about two-fifths basal glabellar width. Palpebral lobes gently arcuate, centred at about glabellar midlength, defined by shallow furrow. Exsagittal length between one-fifth and one-third sagittal glabellar length. Ocular ridges of low relief, poorly-defined. Anterior border furrow of medium width and depth, slight increase in depth in front of glabella. Anterior border convex, gently upturned, of moderate width (sag.). Posterior border very narrow adaxially, widening very gradually abaxially with rounded termination. Furrow defining posterior border wide (exsag.) and of moderate depth, deepest along posterior margin, directed anterolaterally. Course of anterior section of facial suture gently curved forwards to anterior border, then turned more strongly adaxially over border, with overall convergence. Posterior sections strongly divergent and gently curved.

Narrow (tr.) free cheek with gently convex ocular platform. Convex lateral border of moderate width (tr.), gently curved and confluent with long, slender genal spine. Border defined anteriorly by broad, shallow furrow, posteriorly difficult to distinguish from ocular platform. Transverse width of lateral border variable between onethird and one-half that of ocular platform at midlength of palpebral lobe. Exsagittal length of genal spine approximately equal to that of lateral border. Posterior border narrow (exsag.) and short (tr.).

Hypostome moderately convex (tr. & sag.) with elongate middle body that is subrectangular in outline with strongly rounded anterior and posterior margins. Middle furrow shallow and transverse. Sagittal length of anterior lobe between three and four times that of posterior. Maculae strongly developed. Posterior border convex, narrow and approximately straight, defined by wide (sag.) furrow of moderate depth. Lateral border defined by wide furrow that narrows and deepens anteriorly. Lateral border with three sets of small spines. Anterior wings short.

Pygidium gently convex (tr. & sag.), semicircular in outline, sagittal length about two-thirds maximum transverse width. Axis of seven rings and terminal piece tapers moderately backwards. Inter-ring furrows wide (sag.) and curved posteriorly. Axial node development Fig. 54. Trilobites from the Henson Gletscher Formation.

1-6, 10, 11. Kootenia marcoui (Whitfield, 1884). 1a, b, pygidium, partially exfoliated, dorsal and lateral views, MGUH 23396 from GGU collection 301342, x 1.8. 2, damaged cranidium, partially exfoliated, dorsal view, MGUH 23382 from GGU collection 298547, x 1.8. 3, damaged pygidium, partially exfoliated, dorsal view, MGUH 23404 from GGU collection 298547, x 1.4. 4a, b, damaged cranidium, partially exfoliated, dorsal and lateral views, MGUH 23381 from GGU collection 298547, x 2.1. 5, damaged pygidium, partially exfoliated, dorsal view, MGUH 23398 from GGU collection 301342, x 2.1. 6, pygidium, partially exfoliated, dorsal view, MGUH 23406 from GGU collection 298547, x 2.1. 10, damaged pygidium, partially exfoliated, dorsal view, MGUH 23397 from GGU collection 301342, x 2.1. 11, damaged cranidium, partially exfoliated, dorsal view, MGUH 23383 from GGU collection 298547, x 5.5.

7-9, 12-14. Kootenia oscari sp. nov. 7, paratype, damaged pygidium, partially exfoliated, dorsal view, MGUH 23412, x 2.8. 8, paratype, damaged pygidium, partially exfoliated, dorsal view, MGUH 23414 from GGU collection 298547, x 7.7. 9a, b, holotype, pygidium, partially exfoliated, dorsal and lateral views, MGUH 23407, x 2.5. 12, paratype, damaged pygidium, partially exfoliated, dorsal view, MGUH 23413 from GGU collection 298547, x 3.5. 13, paratype, damaged pygidium, partially exfoliated, dorsal view, MGUH 23409, x 3.8. 14, paratype, damaged pygidium, partially exfoliated, dorsal view, MGUH 23411, x 2.8. From GGU collection 301342 unless stated.



variable; maximum development is on anterior four rings, with minimum being a node present on the anterior-most ring only. Posteriorly of last axial node, rings commonly have slight median swellings. Axis defined laterally by narrow axial furrow, posteriorly by change in exoskeletal slope. Posterior of axis joined to pygidial border by short (sag.) medial ridge. In lateral profile axis slopes moderately down to border posteriorly of the



Fig. 55. Trilobites from the Sæterdal Formation.

1-9. 11. Kootenia marcoui (Whitfield, 1884). 1a, b, pygidium, internal mould, dorsal and lateral views, MGUH 23401 from GGU collection 270564, x 2. 2, damaged cranidium. internal mould, dorsal view, MGUH 23378 from GGU collection 270564, x 2. 3. pygidium, internal mould, dorsal view, MGUH 23402 from GGU collection 270564, x 2.5. 4, damaged cranidium internal mould, dorsal view. MGUH 23379 from GGU collection 270590, x 1.1. 5, thoracic seg-ment, internal mould, dorsal view, MGUH 23392 from GGU collection 270564, x 1.8. 6, free cheek, internal mould, dorsal view, MGUH 23386 from GGU collection 270653. x 1.4. 7, damaged pygidium. internal mould, dorsal view, MGUH 23403 from GGU collection 270564, x 1.4. 8. pygidium, internal mould, dorsal view, MGUH 23399 from GGU collection 270590, x 1.2. 9, free cheek, internal mould, dorsal view, MGUH 23387 from GGU collection 270564, x 2.8. 11, pygidium, internal mould, dorsal view, MGUH 23400 from GGU collection 270590, x 1.8.

10, 12, 13. Olenellus cf. O. gilberti Meek, 1874, GGU collection 270584. 10. cephalon, internal mould, dorsal view, MGUH 23229, x 0.9. 12. cephalon, internal mould, dorsal view, MGUH 23230, x 1.1. 13, cephalon, internal mould, dorsal view, MGUH 23231, x 0.9.

third axial ring; anteriorly approximately horizontal. Pleural fields crossed by six wide pleural furrows of medium depth. Pleural furrows reach to border furrow and terminate in shallow pits. Interpleural furrows very weakly impressed or absent. Wide border, flat to very gently convex, defined by broad, shallow furrow. Border of about constant width with slight median indentation. Seven pairs of long, evenly spaced border spines; pairs are all of about equal length, gently curved and directed strongly backwards. Sculpture of the cephalon, hypostome and pygidium is of a coarse reticulate network formed of short ridges and occasional coarse granules. The anterior and lateral borders of the cephalon, and posterior and lateral borders of the hypostome have a sculpture of terrace ridges.

Discussion. – The development of seven pairs of border spines of more-or-less equal length, in combination with the possession of axial nodes, is unusual for species assigned to the widespread and long-ranging genus *Kootenia*. As noted by Palmer in Dutro *et al.* (1984), only nine of the many described species of *Kootenia* have seven pairs of border spines. Blaker (1986: 69) considered this material to represent a new species showing similarities to *K. anabarensis* Lermontova, 1951 and *K. jakutensis* Lermontova, 1951, both of which differ in axial node and spine development (particularly in that the posterior sets of spines are weakly developed in both) and sculpture.

Resser (1938) described K. currieri, K. virginiana and K. browni from Lower Cambrian strata of the Austinville region, Virginia, U. S. A. K. currieri was separated from K. marcoui in terms of pygidial spine morphology, in particular less rapid taper of the spines and wider spacing of the posterior pair. Examination of the type material held at the Natural History Museum, Smithsonian Institution, Washington D. C. reveals no significant differences, and the two species are considered to be conspecific.

Kootenia browni and K. virginiana were distinguished by Resser (1938) on pygidial morphology and, in particular, shorter border spines and shallower pleural furrows in K. browni. Study of the type material indicates that neither of these characters is consistently developed; the two are regarded as synonyms and are also conspecific with K. marcoui.

A large population of *Kootenia marcoui* collected from the Henson Gletscher Formation at Løndal, western Peary Land, illustrates the morphologic variation within the species. Of particular note is that rare specimens reveal the development of an eighth pair of small spines situated immediately behind the axis. Although not commonly developed, their presence is often indicated by marginal swellings or nodes.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, 11, localities 1 and 6). Sæterdal Formation, (Fig. 8B). Age: Early Cambrian, *Olenellus* Zone.

Kootenia oscari sp. nov.

Figs 49.3, 9; 54.7-9, 12-14

1964 Genus and species undetermined 1, Palmer, p. F11, pl. 3, fig. 16.

1986 Bonnia sp. nov., Blaker, p. 69.

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Derivation of name. – For State Geologist Niels ('Oscar') Henriksen, leader of the North Greenland Project (1978-85).

Holotype. – Pygidium; MGUH 23407 from GGU collection 301342 (Fig. 54.9a, b).

Figured paratypes. – Pygidium; MGUH 23408-23412 from GGU collection 301342, MGUH 23413-23414 from GGU collection 298547.

Other material. - GGU collections 298547 and 301342.

Diagnosis. – Pygidial border with two pairs of spines, posterior pair of considerably greater length. Axis of five well-defined rings, occasionally a weakly-defined sixth. Five pairs of pleural furrows.

Description. - Pygidium gently convex (tr. & sag.), semicircular in outline. Axis formed of five clearly-defined rings and terminal piece; ill-defined sixth ring occasionally evident. Axis tapers gradually backwards, joined to border by medial ridge. Axial rings of moderate convexity (tr.), without median node. Inter-ring furrows decrease in width (sag.) backwards, variable from straight to gently concave posteriorly. Axial furrow narrow (tr.) and of moderate depth. Gently convex pleural fields crossed by five pairs of wide pleural furrows. Anterior pair of pleural furrows deepest and continuous across border; almost reaching to outer margin. Narrow interpleural furrows only evident on small pygidia (see Fig. 54.8). Convex border attains greatest width at position of second pair of spines, narrows posteriorly. Border furrow broad and of moderate depth, with slight shallowing anteriorly. Two pairs of border spines; anterior pair short, slender and curved gently posterolaterally. Posterior pair with wide base, considerably longer than anterior pair and directed backwards. Only observed sculpture is weakly-defined terrace lines on border.

Discussion. – Blaker (1986: 69) reported this taxon as a new species of *Bonnia*. In the light of discussion above (see also *Ogygopsis*), it is now concluded that the pygidial morphology indicates reference not to *Bonnia* but to *Kootenia*. This conclusion is based on the combination of 5 or 6 axial rings forming the pygidial axis (two or three rings being typical of *Bonnia* species), the considerable length of the second pair of border spines (when developed on *Bonnia* species the second set of spines are always short) and the strong semicircular outline to the pygidium.

Only a few described species of *Kootenia* have two pairs of pygidial border spines. *K. mendosa* Resser, 1939. is distinctly different from *K. oscari* in that both pairs of spines are very short, there are only four pairs of pleural furrows, and the axis is formed of two or three clearly-defined rings and a long (sag.) terminal piece. In all these features the species is more closely akin to *Bonnia. K. romensis* Resser, 1938 is also more typical of forms assigned to *Bonnia*, with only two axial rings and the terminal piece forming the axis, and three pairs of pleural furrows. This combination of characters makes *K. romensis* easily distinguishable from *K. oscari*.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, locality 1) Age: Early Cambrian, *Olenellus* Zone.

Kootenia radiata sp. nov.

Figs 56; 57.1-4, 6, 7

Derivation of name. – From the latin *radiatus*, referring to the radial arrangement of pygidial spines.

Holotype. – Pygidium; MGUH 23415 from GGU collection 301351 (Fig.57.3).

Figured paratypes. – Cranidium; MGUH 23416-23420 from GGU collection 301351. Free cheek; MGUH 23421 from GGU collection 301351. Hypostome; MGUH 23422-23423 from GGU 301351. Pygidium; 23324-23328 from GGU collection 301351.

Other material. - GGU collection 301351.

Diagnosis. – Long (sag.), narrow (tr.) pygidial axis of five or six rings. Five pairs of pleural furrows. Border with five pairs of slender spines. Coarse reticulate sculpture on axis and pleural fields, border with medium sized granules.



Fig. 56. *Kootenia radiata* sp. nov. Henson Gletscher Formation. 1, paratype, cranidium, dorsal view, MGUH 23416, x 7. 2, paratype, damaged cranidium, dorsal view, MGUH 23420, x 7. 4, paratype, cranidium, dorsal view, MGUH 23420, x 5. 5, paratype, damaged cranidium, dorsal view, MGUH 23420, x 5. 5, paratype, damaged cranidium, dorsal view, MGUH 23418, x 4. 6, paratype, pygidium, latex of external mould, dorsal view, MGUH 23426, x 5. 7a, b, paratype, cranidium, lateral and dorsal views, MGUH 23419, x 4. 8, paratype, hypostome, ventral view, MGUH 23423, x 5.5. All from GGU collection 301351.



Fig. 57. Trilobites from the Henson Gletscher Formation.

1-4, 6, 7. *Kootenia radiata* sp. nov. 1, paratype, damaged pygidium, latex of external mould, dorsal view, MGUH 23424, x 3.5. 2, paratype, free cheek, dorsal view, MGUH 23421, x 5. 3, holotype, pygidium, latex of external mould, dorsal view, MGUH 23415, x 4. 4, paratype, pygidium, partially exfoliated, dorsal view, MGUH 23427, x 3. 6, paratype, pygidium, partially exfoliated, dorsal view, MGUH 23428, x 3.5. 7, paratype, damaged pygidium, partially exfoliated, dorsal view, MGUH 23425, x 5. All from GGU collection 301351.

5, Kootenia cf. K. 'longa' Ju, 1983, pygidium, internal mould, dorsal view, MGUH 23442 from GGU collection 301351, x 7.5.

Description. – Glabella strongly convex (tr. & sag.), with glabellar sides of about equal convergence backwards and forwards of midlength. Marked contraction of glabellar sides at intersection with ocular ridges. Glabella anterior bluntly curved; reaches to anterior border furrow. Glabellar furrows not developed, though on some specimens faint outlines of muscle scars evident. Axial furrows deep and narrow (tr.), shallowing anteriorly and posteriorly from widest part of glabella. Gently convex (tr.) palpebral areas with maximum width approximately

one-half basal glabellar width. Palpebral lobes of moderate length; defined by furrow that shallows over midlength of lobe. Exsagittal length of lobes about one-third sagittal glabellar length. Ocular ridges low, without clearly defined furrows. Preocular areas of fixed cheek slope strongly down to narrow anterior border furrow, which widens and deepens in front of glabella. Anterior border gently curved, strongly convex (exsag.), and slightly upturned sagittally. Occipital furrow variable from straight to curved moderately posteriorly, deepest abaxially, with notable widening and shallowing adaxially. Occipital ring gently convex (tr.) with faint development of median node on posterior margin. Wide (tr.), narrow (exsag.) posterior area of fixed cheek. Posterior border furrow widens and deepens abaxially. Posterior border very narrow adaxially, widest at fulcrum, terminations rounded. Anterior section of facial suture initially convex abaxially and divergent from palpebral lobe to anterior border, then turned adaxially over border with overall divergence. Posterior sections gently curved but very strongly divergent.

Free cheek with wide (tr.) gently convex ocular platform, separated from lateral border by an indistinct furrow, that is of greatest definition anteriorly. Lateral border of moderate transverse convexity and width, widening slightly posteriorly and continuous with short genal spine. Posterior border very short (tr.) and poorly defined.

Subrectangular hypostome with elongate middle body clearly defined into anterior and posterior lobes. Anterior lobe inflated and ovate in outline, with very prominent maculae. Posterior lobe crescentic in outline, at a lower elevation than anterior lobe. Border narrow, convex and posteriorly almost straight, defined by narrow, deep furrow which widens anterolaterally. Anterior wings short and prong-like.

Pygidium semicircular in outline, gently convex transversely and longitudinally. Sagittal length between twothirds and three-quarters maximum transverse width. Axis with gradual taper posteriorly; anterior width up to one-third that of pygidium. Axis of five or six, clearly-defined rings and terminal piece. Axial furrow of moderate width (tr.) and depth, posterior of axis arises abruptly from inner margin of border. Inter-ring furrows wide (sag.) and shallow, narrowing abaxially. Pleural fields crossed by four or five wide pleural furrows, deepest distally and shallowing adaxially, reaching to border furrow. Anterior pleural furrow continues across the border furrow to spine base. Shallow interpleural furrows apparent only on small specimens. Pygidial border gently convex, of moderate width and defined by furrow of variable depth, with slight pits at pleural and pleural furrow terminations. Five pairs of border spines positioned opposite terminations of pleural furrows. Spines slender and of moderate length, directed progressively more strongly backwards. Spines not evenly spaced with greatest separation between second and third pairs. Posterior pair short, slender and for small specimens situated immediately behind axial furrows; more distally situated as pygidial size increases.

Sculpture of coarse terrace ridges on the cranidial anterior border and lateral border of free cheek. All other parts of cranidium with a closely-spaced reticulate sculpture of ridges, which is also found on the middle body of the hypostome and pleural fields and axis of pygidium. Free cheek and pygidial border with widely-spaced medium granules. Discussion. – As noted previously, new material of *Kootenia* frequently differs from any of the described species even though the number of species assigned to the genus is considerable. This species with 5 pairs of border spines from North Greenland is one such example. Comparisons with the described species of *Kootenia* that have five pairs of spines demonstrate that this species differs consistently by a combination of the number and morphology of axial rings, the number of pleural furrows and sculpture.

Kootenia diutina Fritz, 1972 differs from K. radiata in the development of axial nodes on the anterior three rings, one fewer pair of pleural furrows and very short border spines, with the fifth pair represented by only slight swellings. K. florens Suvorova, 1964 has an axis of only four rings, all with axial nodes, and pleural fields crossed by only four pairs of pleural furrows, as does K. pirumata Lu in Lu et al. 1965.

Of the remaining species, four were described by Resser (1939); K. convoluta, K. granulosa, K. bearensis and K. maladensis are all distinguished from this new species of Kootenia by having three axial rings and pleural fields crossed by three or four pairs of pleural furrows. K. maladensis was distinguished from K. granulosa by Resser (1939) by its lack of granular sculpture and narrower (sag.) anterior border in front of the glabella. An examination of the type pygidium of K. maladensis reveals there to be granular sculpture on the pleural fields and differences of the cranidium are also not substantiated. Further, K. granulosa was distinguished from K. convoluta on very minor differences of both cranidium and pygidium. The type material of all three species was found in association, and it is concluded that they are synonymous. Also occurring with this material is a single cranidium that Resser (1939) referred to the new species K. nitida. Cited differences from K. granulosa were a narrower glabella with deeper glabellar furrows and deeper axial furrows, particularly anteriorly; these are most probably accounted for by intraspecific variation and K. nitida is also regarded as being conspecific. K. bearensis is also placed in synonomy since it is not consistently different in any morphological feature.

Kootenia pectenoides was also described by Resser (1939) as having five pairs of pygidial border spines; in fact it has six.

Kootenia amonoi Kobayashi, 1961 differs in the development of only three axial rings and pairs of pleural furrows, with border spines that are short and stout. Four species described by Ergaliev *et al.* (1977) from southern Kazakhstan can also be distinguished on fewer axial rings and pleural furrows, as can *K. crassinucha* Fritz, 1968 from the Middle Cambrian of Nevada and *K. modica* (Whitehouse, 1939) and *K. fergusoni* (Gregory, 1903) from the Lower Cambrian of north-eastern Australia. Similar distinctions can be made for *K. rasilis* Suvorova, 1964 and *K. pricei* Resser, 1938, both of which have four axial rings and pleural furrows. Very short border spines characterise *K. asiatica* Kobayashi, 1935 which has five axial rings, with axial nodes on at least the anterior four.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Kootenia sagena sp. nov.

Figs 58; 59.1, 3, 4

Derivation of name. – From the Latin *sagena*, referring to the net-like sculpture.

Holotype. – Pygidium; MGUH 23429 from GGU collection 271756 (Fig. 58.5a, b).

Figured paratypes. – Cranidium; MGUH 23430 from GGU collection 271756, MGUH 23431 from GGU collection 225704, MGUH 23432-23433 from GGU collection 225703. Pygidium; 23434-23437 from GGU collection 271756, MGUH 23438 from GGU collection 225703. Free cheek; MGUH 23439 from GGU collection 225703. Hypostome; MGUH 23440-23441 from GGU collection 271756. Complete specimen; MGUH 23442 from GGU collection 271756.

Other material. – GGU collections 218608, 225702, 225703, 271745, 271756.

Diagnosis. – Generally strongly convex (tr. & sag.) glabella without furrows. Anterior border strongly upturned. Occipital ring with moderately long, slender occipital spine. Pygidium with axis of four clearly-defined rings, of which anterior two or three have well-developed axial spines. Pygidial margin with up to three pairs of short

Fig. 58. Kootenia sagena sp. nov. Henson Gletscher Formation. 1, paratype, meraspid cranidium, dorsal view. MGUH 23430 from GGU collection 271756, x 8.5. 2, paratype, cranidium, dorsal view, MGUH 23432 from GGU collection 225703, x 4.9. 3, paratype, pygidium, dorsal view, MGUH 23435 from GGU collection 271756, x 4.2. 4a, b, paratype, pygidium, dorsal and lateral views, MGUH 23437 from GGU collection 271756, x 7. 5a, b, holotype, pygidium, dorsal and lateral views. MGUH 23429 from GGU collection 271756, x 6.1. 6a, b, paratype, damaged cranidium, dorsal and lateral views, MGUH 23431 from GGU collection 225704, x 4.9. 7, paratype, complete specimen, dorsal view, MGUH 23442 from GGU collection 271756, x 5.6. 8, paratype, free cheek, dorsal view, MGUH 23439 from GGU collection 225703, x 7. 9. paratype, hypostome, partially exfoliated, ventral view, MGUH 23440 from GGU collection 271756, x 5.6. 10, paratype, pygidium, dorsal view, MGUH 23436 from GGU collection 271756, x 6.3. 11a, b, paratype, cranidium, dorsal and lateral views, MGUH 23433 from GGU collection 225703, x 4.9.



spines; normally only two pairs developed. Glabella, fixed cheeks and pygidial axis with coarse network of ridges.

Description. - Prominent glabella moderately to strongly convex (tr. & sag.). Glabellar sides variable from subparallel to moderately convex, with about equal convergence forwards and backwards of the midlength. Anterior of glabella gently curved, reaches to anterior border furrow. Glabella unfurrowed, although faint impressions of muscle scars on some specimens (see Fig. 58.6a, b). Occipital furrow gently curved posteriorly, deep distally with considerable shallowing axially, and slight widening (sag.). Occipital ring strongly convex (tr.) with slender median spine of moderate length on posterior margin. Sagittal length of occipital ring approximately one-seventh that of glabella. Anterior border strongly upturned, wide (sag.) with broadly curved anterior margin; defined by deep furrow. Well- defined, short (exsag.) palpebral lobes centred slightly posteriorly of glabellar midlength. Pronounced ocular ridges defined by shallow furrow posteriorly, anteriorly by distinct change in exoskeletal slope. Narrow (exsag.) preocular areas of fixed cheek slope down rapidly to anterior border furrow. Narrow (exsag.) posterior border defined by deep furrow. Initially border directed weakly posterolaterally to fulcrum, then strongly downturned; terminations rounded. Anterior sections of facial suture with overall slight convergence, posterior sections strongly divergent.

Free cheek with narrow (tr.) ocular platform and wide (tr.) border that is distinctly upraised above the ocular platform, from which it is separated by a shallow furrow. Lateral border extends into short, stubby genal spine.

Hypostome subrectangular in outline with ovate middle body and short prong-like anterior wings. Strongly convex (tr. & sag.) anterior lobe with distinct maculae posteriorly. Posterior and lateral borders narrow, defined by narrow, deep furrow. Lateral border with several pairs of short spines.

Thorax known from partially enrolled meraspid (Fig. 58.7). Axial rings moderately convex (tr.) with median spine on at least the anterior-most ring. Axis laterally defined by narrow furrow of moderate depth. Transverse width of ring about one-third that of segment. Pleurae with deep and wide (exsag.) pleural furrows, and rounded terminations.

Pygidium semicircular in outline with sagittal length two-thirds maximum transverse width. Prominent axis tapers gradually backwards, defined laterally by narrow furrow that shallows posteriorly; the posterior of the axis being defined by a rapid change in exoskeletal slope. Axis with four rings which are clearly defined, rarely an ill-defined fifth, and a terminal piece. Inter-ring furrows shallow over axial line. Anterior two or three rings with prominent median spines In lateral profile the spines are almost vertical, being curved only very slightly backwards. Pleural fields crossed by four pairs of pleural furrows of moderate width and depth. Interpleural furrows



Fig. 59. Trilobites from the Henson Gletscher Formation.

1, 3, 4, *Kootenia sagena* sp. nov. 1a, b, paratype, pygidium, dorsal and posterior views, MGUH 23434 from GGU collection 271756, x 5.4. 3, paratype, pygidium, lateralview, MGUH 23438 from GGU collection 225703, x 4.2. 4, paratype, hypostome, ventral view, MGUH 23441 from GGU collection 271756, x 6.3.

2, 5, *Olenellus* cf. *O. truemani* Walcott, 1913. 2, hypostome, partially exfoliated, ventral view, MGUH 23280 from GGU collection 271756, x 3.5. 5, damaged cephalon, partially exfoliated, dorsal view, MGUH 23277 from GGU collection 271756, x 2.1.

very faintly impressed or absent. Border narrows anterolaterally, gently convex with a weak median indentation (Fig. 59.1a), equivalent to an elevation in posterior aspect (Fig. 59.1b). Variable morphology to the lateral margin; anterolaterally a distinct pair of spines are consistently developed and posteriorly a further two pairs vary from being well-formed to being represented by only slight swellings of the outer margin.

Sculpture of the glabella and palpebral areas consists of a coarse polygonal network of ridges, whilst the anterior border possesses wide terrace ridges which are also to be found on the lateral border and spine of the free cheek, and pygidial border. The pygidial axis has coarse raised ridges, with a more subdued arrangement on the pleural fields. This subdued sculpture is also found on the middle body of the hypostome.

Discussion. – *Kootenia sagena* differs from *K. radiata* in having a more strongly convex glabella and a strongly upturned anterior brim.

The glabella in the meraspid cranidium of *K. sagena* (Fig. 58.1) expands rapidly forwards with a bluntly rounded anterior. Two pairs of glabellar furrows are well impressed, both reach the axial furrow but do not cross the glabella. S1 of moderate length and depth, directed backwards at about 70 degrees to an exsagittal line. S2 considerably shorter, of about equal depth but directed backwards at a smaller angle. No differentiation into ocular ridge and palpebral lobe, and occipital furrow of equal depth and width throughout.

For holaspid specimens the most variable features are in the pygidium, with the number of axial spines (1-3) and lateral border spines (1-3) differing through the populations. It has not been possible to establish any correlations between the relative numbers of each, and this material is interpreted as a single, variable species.

This species presents a taxonomic problem; arguments exist for an assignment to either Bonnia Walcott, 1916 or to Kootenia. Fritz (1972: 31) stated that the genus Bonnia was composed of "... small dorypygid trilobites, with thick, usually rather smooth tests." With such a diagnosis, the very strong sculpture of this species from North Greenland would be unusual for the genus. Fritz (1972: 32) continued that "Kootenia resembles Bonnia", differentiating Kootenia on its generally larger size, and for most species the possession of five to seven pairs of well-developed pygidial border spines, as opposed to the usual one pair in Bonnia species. Although this species has rather few pygidial pleural ridges, it is assigned to Kootenia because of the outline of the glabella and pygidial axis, presence of axial spines and the incipient development of several pairs of pygidial border spines.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 11, localities 5 and 6). Age: Early Cambrian, *Olenellus* Zone.

Kootenia cf. K. 'longa' Ju, 1983

Fig. 57.5

cf. 1983 Kootenia longa Ju, p. 631, pl. 3, figs 1-4

Figured material. – Pygidium; MGUH 23443 from GGU collection 301351.

Other material. - GGU collection 301351.

Remarks. - This form from North Greenland most closely resembles Kootenia 'longa' Ju, 1983 (a junior homonym; Repina et al. 1964 also described a species of this name) from the Lower Cambrian of Zhejiang, China. Only a single pygidium of K. 'longa' was illustrated and this is comparable to the Greenland specimen in showing four well-defined axial rings, an ill-defined fifth pair, and four pairs of pleural furrows. Differences are that the border of K. 'longa' has two short denticles, with the third pair of spines represented by only slight swellings. Although the spines are not preserved on the specimens from Freuchen Land, it is evident from the broken bases that all three were well-developed and stout, at least at the base. These features readily distinguish K. cf. K. 'longa' from K. radiata sp. nov., with which it occurs.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone

Kootenia sp. A

Fig. 42.1, 7

Figured material. – Pygidium; MGUH 23444-23445 from GGU collection 271428.

Description. – Pygidial axis consists of three rings, a faint fourth, and terminal piece. Anterior ring may possess median axial spine. Pleural fields crossed by three sets of pleural furrows, and two weakly-defined pairs of interpleural furrows. Border furrow wide and of moderate depth, deepest at intersections of pleural furrows. Border rather flattened, bearing six pairs of spines. All pairs slender, of moderate length and about equally spaced. Sculpture of closely-spaced medium sized granules on the pygidial spines.

Remarks. – This form is referred to *Kootenia* on the basis of its overall morphology. As it is known from only two pygidia, no assignment is possible to any one of the more than 50 described species of the genus that have six pairs of border spines.

Occurrence in North Greenland. – Henson Gletscher Formation, (Fig. 8A, locality 3). Age: Early Cambrian, *Olenellus* Zone.

Kootenia sp. B

Fig. 20.3

Figured material. – Pygidium; MGUH 23446 from GGU collection 315051.

Description. – Pygidium semicircular in outline, with prominent, convex axis, reaching to border furrow. Axis of five rings and terminal piece, tapers gently backwards. Pleural fields crossed by three pairs of pleural furrows; interpleural furrows are faintly defined. Narrow border defined by broad furrow that narrows posteriorly. Border with four pairs of evenly-spaced, short spines.

Remarks. – This form is represented by a solitary specimen which, due to its size, is probably a meraspid.

Occurrence in North Greenland. – Kap Troedsson Formation, (Fig. 8A, locality 4). Age: Early Cambrian, *Olenellus* Zone.

Dorypygidae genus and species undetermined A

Fig. 49.1, 2, 6, 7

Figured material. – Cranidium; MGUH 23447-23448 from GGU collection 301340. Pygidium; MGUH 23449-23450 from GGU collection 301340.

Other material. - GGU collection 301340.

Description. - Glabella rectangular in outline, lateral margins converging very slightly forwards from SO. Glabella defined by wide (tr.) furrows of moderate depth. Anterior of glabella almost straight and reaching to anterior border furrow. Three pairs of glabellar furrows; S1 straight and directed backwards at about 50 degrees to an exsagittal line, of moderate depth. S2 directed backwards at similar angle to S1, shorter and very shallow close to axial furrow. S3 short and transverse, isolated from axial furrow. SO wide (sag.) and shallow, distally deeper with slight narrowing. Occipital ring moderately convex with sagittal length approximately one-tenth that of glabella. Short median spine directed backwards from posterior margin of ring. Narrow (tr.) palpebral areas about onehalf basal glabellar width. Palpebral lobes wide (tr.) and short (exsag.) with length approximately one-quarter sagittal glabellar length. Lobes gently arcuate, centred at

about midlength of L2, defined by broad (tr.) shallow furrow that is confluent with narrow furrow defining posterior margin of ocular ridge. Pronounced ocular ridges defined anteriorly by change in exoskeletal slope. Preocular areas of fixed cheek slope moderately anterolaterally. Wide (sag.) anterior border defined distally by shallow furrow with marked deepening in front of glabella. Border gently convex, upturned, with curved anterior margin. Posterior border furrow of moderate width and depth, defines narrow border. Anterior sections of facial suture initially gently convex abaxially until border, then turned strongly adaxially over border. Posterior section not known.

Gently convex, semicircular pygidium with narrow (tr.) axis tapering gently posteriorly and reaching to, or almost to, border furrow. Anterior width of axis approximately one-quarter maximum pygidial width. For the specimen with the greatest sagittal length the axis is formed of six well-defined rings, a poorly-impressed seventh and terminal piece. The axes of smaller specimens have only five well-defined rings. Axial rings without spine or node, defined by straight inter-ring furrows. Axis defined laterally by furrow of variable width and depth, posterior of axis defined by exoskeletal slope change. Gently convex (tr.) pleural fields crossed by up to six pairs of very shallow interpleural furrows whose terminations in the border furrow are marked by depressions, and in the axial furrow by deep slits that extend across the axial furrow to merge with the inter-ring furrows. Pleural furrows wide (exsag.) and of moderate depth, terminating as pits in the border furrow. Border furrow rather indistinct, except around the posterior, defines convex border with four pairs of spines of approximately equal spacing. Anterior three pairs short and directed posterolaterally. Fourth pair very long, gently curved, directed backwards and marked by deep median furrow. Posterior pair of spines positioned widely apart.

All parts of exoskeleton without apparent sculpture.

Discussion. – The pygidium of this genus shows some similarities to the Middle Cambrian *Dorypyge* Dames. 1883 which is characterised by one pair of long border spines and several short pairs. However, pygidia of almost all species of *Dorypyge* have five pairs of border spines, with the fifth pair being of greatest length. Additionally, species of *Dorypyge* also differs in cranidial characteristics; the genus is characterised by a glabella that converges backwards and forwards of the widest (tr.) point, a strongly rounded anterior and furrows that are poorly-defined or absent.

Olenoides encompasses a wide range of morphologies, particularly in terms of the pygidium, and it is with this genus that the present material shows most affinities. The North Greenland form differs from typical species of Olenoides in the narrow (tr.) axis formed of seven rings, the wide spacing of the posterior pair of border spines and well-defined posterior border. Olenoides is typified by a broad (tr.) axis of 3-5 rings and an ill-defined pygidial border, with the posterior pair of spines closely spaced and not of such considerable length. The cranidium in the Greenland material, particularly the glabella, also differs from typical species of *Olenoides*, although it does have a similarly shaped glabella to *Olenoides brevispinus* Rasetti, 1948 from Middle Cambrian conglomerates at Lévis, Quebec, Canada. Differences are that the anterior margin of *O. brevispinus* is more strongly rounded, S1 is not directed as strongly backward and the glabellar sides are initially convergent until the level of S1, diverging forwards of S2. The associated pygidium of *O. brevispinus* is distinctly different, having an axis of four rings and a terminal piece, and pleural fields crossed by four pairs of pleural furrows.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Family Dolichometopidae Walcott, 1916 Genus Athabaskiella Kobayashi, 1942

Diagnosis. – After Robison (1988: 62). Dolichometopid with narrow continuous anterior border on cranidium. Glabella expanding forward in anterior half; having four pairs lateral furrows, S1 deepest and strongly oblique backwards. Palpebral lobe of medium length, slightly posterior from glabellar midlength. Pygidium cordiform to triangular; axis usually about half pygidial length, having 1 or 2 rings and terminal piece; pleural region concave, border not differentiated.

Athabaskiella? sp. A

Fig. 61.9

Figured material. – Cranidium; MGUH 23583 from GGU collection 315112.

Description. – Glabellar sides very slightly divergent from SO forwards to level of S2, expanded rapidly forwards of S2 with very gently curved anterior. Glabella gently convex (tr. & sag.) with four pairs of lateral furrows; all pairs except S3 reach axial furrow. S1 deep and of moderate length, directed strongly backwards; S2 considerably shallower and shorter, almost transverse; S3 very faintly impressed, short and directed moderately forwards; S4 of similar orientation to S3, but of slightly greater depth and length. SO with slight forwards deflection over sagittal line, wide (exsag.) and shallow, with slight deepening abaxially. Long (exsag.) occipital ring with gently curved posterior margin, exsagittal length one-fifth that of glabella. Glabella laterally defined by

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narrow (tr.) furrow, deepest at level of S2. Anterior border and furrow exceptionally narrow in front of glabella, wider abaxially. Narrow and moderately convex (tr.) palpebral areas. Palpebral lobes long (exsag.) and gently arcuate, no obvious differentiation into ocular ridge; palpebral furrow of moderate width and depth. Exsagittal length of lobes about one-half sagittal glabellar length.

Discussion. – This form is similar to specimens assigned by Robison (1988) to *Athabaskiella obsoleta* (Raymond, 1937) from the late Middle Cambrian Holm Dal Formation in Freuchen Land, North Greenland. It differs primarily from Robison's material in that the anterior expansion of the glabella is not as pronounced, S1 is straight and not as strongly impressed, and the axial furrows do not show initial rapid convergence forwards of SO.

As noted by Robison (1988: 62), all reported occurrences of the genus are from the late Middle Cambrian *Lejopyge laevigata* Zone. Hence, this identification, which would otherwise significantly extend the known stratigraphical range to the Early Cambrian *Olenellus* Zone, is tentative.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A. 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Family Zacanthoididae Swinnerton, 1915

Remarks. – As discussed by Palmer (in Palmer & Halley 1979: 85), the Zacanthoididae as defined by Henningsmoen (in Moore 1959: 227) includes a variety of corynexochid forms that are typified by spinose pygidia, and a long slender glabella that is expanded anteriorly. Palmer suggested that the small-eyed genera now included in the Zacanthoididae should be removed to a separate family or subfamily. By so doing, the Zacanthoididae would then be characterised by long, arcuate palpebral lobes.

Genus Zacanthopsis Resser, 1938

Type species. – By original designation; *Olenoides levis* Walcott, 1886, p. 187, pl. 25, figs 3, 3a from the Lower Cambrian at Pioche, Nevada, U. S. A.

Diagnosis. – Emended from Resser (1938). Cranidium subquadrate; long (sag.) glabella expands anteriorly, gently curved across front with four pairs glabellar furrows. Occipital ring with slender spine. Frontal area of cranidium upturned. Long (exsag.) palpebral lobes, strongly curved and reaching back to level of SO. Small pygidium with broad (tr.) axis of three or four rings. Poorly-defined border with three or four pairs of short spines. Sculpture of closely-spaced granules.

Zacanthopsis levis (Walcott, 1886)

Figs 60.1, 3, 4, 6, 7; 61.4, 5

- 1886 Olenoides levis Walcott, p. 187, pl. 25, figs 3, 3a.
- 1938 Zacanthopsis virginica n. sp., Resser, p. 106, pl. 3, figs 39, 48.
- 1948 Zacanthopsis virginica Resser; Rasetti, p. 21, pl. 2, figs 17-19.
- 1968 Zacanthopsis levis (Walcott); Fritz, p. 217, pl. 36, figs 11-14. (Includes complete synonomy)

Type material. – Type series USNM 15445 in the Natural History Museum, Smithsonian Institution, Washington D. C., from Pioche, Nevada, U. S. A.

Figured material. – Cranidium; MGUH 23451-23457 from GGU collection 301346.



Fig. 60. Trilobites from the Henson Gletscher Formation.

1, 3, 4, 6, 7. Zacanthopsis levis (Walcott, 1886). Ia, b, cranidium, partially exfoliated, dorsal and lateral views, MGUH 23453, x 3.5. 3, cranidium, partially exfoliated, dorsal view, MGUH 23457, x 4.5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23456, x 5. 6, damaged cranidium, partially exfoliated, dorsal view, MGUH 23456, x 5. 6, damaged cranidium, partially exfoliated, dorsal view, MGUH 23456, x 5. 7, damaged cranidium, partially exfoliated, dorsal view, MGUH 23456, x 5. 7, damaged cranidium, partially exfoliated, dorsal view, MGUH 23457, x 4.5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23456, x 5. 7, damaged cranidium, partially exfoliated, dorsal view, MGUH 23457, x 4.5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23457, x 4.5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23457, x 4.5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23457, x 4.5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23457, x 4.5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23457, x 4.5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23457, x 4.5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23457, x 5.7, damaged cranidium, partially exfoliated, dorsal view, MGUH 23451, x 5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23451, x 5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23451, x 5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23451, x 5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23451, x 5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23451, x 5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23451, x 5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23451, x 5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23451, x 5. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23451, x 5. 4, damaged cranidium, partially exfoliated, dorsal

2, 5, 8. *Stephenaspis? avita* Palmer, 1964. 2, cranidium, partially exfoliated, dorsal view, MGUH 23468, x 11. 5, cranidium, partially exfoliated, dorsal view, MGUH 23467, x 10.5. All from GGU collection 301340.

Other material. – GGU collections 298547, 298553, 301340, 301346, 301349 and 315112.

Description. - Cranidium subquadrate in outline with elongate glabella. Glabella moderately convex transversely, gently convex longitudinally, with subparallel sides until level of S2, diverging between S2 and S4 and gently rounded anterior. Four pairs of glabellar furrows of variable impression; S1 most strongly developed, short, shallow and directed moderately backwards, reaches axial furrow. S2 formed by shallow pits that are connected to the axial furrow, may be transverse or directed backwards; on some specimens position of S2 marked by contraction of glabellar sides. S3 variably developed, shallow furrow directed forwards, or barely apparent as small pits. S4 transverse or inclined slightly forwards, short and shallow. Occipital furrow straight, or curved gently posteriorly, formed of deep, elongate pits distally, considerably shallower adaxially. Wide (sag.) occipital ring with long slender medial spine that is directed gently upwards and backwards. Sagittal length of occipital ring (including spine) approximately two-fifths that of glabella; exclusive of occipital spine slightly less than one-fifth. Glabella does not reach to border furrow, but is separated from it by preglabellar field of variable sagittal length. Preocular cheek initially slopes down strongly anterolaterally, then moderately upturned. A low, narrow parafrontal band parallels the front of the glabella terminating at the ocular ridges. Parafrontal band separated from glabella by shallow furrow. Palpebral areas gently convex (tr.). Transverse width of palpebral area slightly less than basal glabellar width. Palpebral lobes long (exsag.), strongly curved, highly convex, moderately wide (tr.), and well-defined by deep palpebral furrows. Lobes tilt strongly inwards with steep lateral margins; exsagittal length approximately one-third sagittal glabellar length (inclusive of spine). Ocular ridges narrower and at lower elevation than lobes, defined posteriorly by shallow furrow that is confluent with palpebral furrow; anteriorly by change in exoskeletal slope. Posterior of palpebral lobe reaches almost to posterior border furrow. Anterior border wide (sag.), highly convex and defined distally by shallow furrow, in front of glabella by change in exoskeletal slope. Posterior border very narrow axially, widening very slightly over abaxial half to point of geniculation, then sharply downturned with rounded tip. Posterior border furrow shallow axially, widening and deepening distally. Anterior sections of facial suture divergent from palpebral lobe to anterior border, then turned gently inwards over anterior border. Course of posterior sections not known. Sculpture of the anterior border is of terrace ridges which vary from prominent to just apparent. All other parts of cranidium with closely-spaced, medium to coarse granules. Caecal veins radiate across the frontal area to the anterior border from the glabella and ocular ridges.

Remarks. – Zacanthopsis virginica Resser, 1938 from the Lower Cambrian of Virginia was distinguished from Z.

levis by a more strongly curved anterior margin, a wider (sag.) anterior border, greater impression of glabellar furrows, and a more strongly expanded anterior glabellar lobe. Rasetti (1948) subsequently assigned material from Quebec, Canada, to Z. *virginica* noting the variable morphology of this species, particularly the depth of the glabellar furrows, curvature of the palpebral lobes and the transverse width of the palpebral areas. The material from Freuchen Land shows variability in all of the characters cited by Resser (1938) as being distinct in Z. *virginica*, and it is concluded that Z. *virginica*, falling within the range of morphological variation of Z. *levis*, is its junior synonym.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Zacanthopsis contracta Palmer, 1964

Figs 61.6-8; 77.5, 6

- 1964 Zacanthopsis contractus n. sp., Palmer, p. F10, pl. 3, figs 4-6.
- 1972 Zacanthopsis stribuccus sp. nov., Fritz, p. 38, pl. 16, figs 19-20.

Type material. – Holotype cranidium USNM 144287, Natural History Museum, Smithsonian Institution, Washington D. C., from the Lower Cambrian Saline Valley Formation, 8 km north-east of Gold Point, Esmeralda County, Nevada, U. S. A.

Figured material. – Cranidium; MGUH 23458-23460 from GGU collection 298544, MGUH 23461 from GGU collection 315097, MGUH 23462 from GGU collection 301343.

Other material. - GGU collections 298544 and 315097.

Diagnosis. – After Palmer (1964: F10). Species of Zacanthopsis in which the width between anterior sections of facial sutures is considerably less than width between lateral margins of palpebral lobes. Occipital ring with short slender spine. Axial part of glabella with fine closelyspaced granules.

Description. – Cranidium subquadrate in outline, with prominent glabella that has subparallel or gently divergent sides between SO and S2, forwards of S2 more strongly divergent; anterior gently curved. Glabella moderately convex (tr. & sag.) with four pairs of furrows, all reach to the axial furrow. S1 of variable length, short, deep incisions directed strongly backwards, and occasionally connected across glabella by very poorly-defined furrow. S2 transverse, or directed gently forwards,



Fig. 61. Trilobites from the Henson Gletscher Formation.

1. Corynexochid genus and species undetermined A. Damaged pygidium, dorsal view, MGUH 23597 from GGU collection 301340, x 8.5.

2, 3. Zacanthoides? sp. A. 2, cranidium, partially exfoliated, dorsal view, MGUH 23464, x 8. 3, cranidium, latex of external mould, dorsal view, MGUH 23465, x 9. Both from GGU collection 301340.

4, 5, Zacanthopsis levis (Walcott, 1886). 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23455, x 5.5. 5a, b, damaged cranidium, partially exfoliated, dorsal and lateral views, MGUH 23454, x 4. Both from GGU collection 301346.

6⁻⁸. Zacanthopsis contracta Palmer, 1964. 6, damaged cranidium, dorsal view, MGUH 23459 from GGU collection 298544, x 13.5. 7, damaged cranidium, dorsal view, MGUH 23460 from GGU collection 298544, x 11. 8, damaged cranidium, dorsal view, MGUH 23461 from GGU collection 315097, x 8.

9. Athabaskiella? sp. A. Cranidium, dorsal view, MGUH 23583 from GGU collection 315112, x 8.5.

of similar depth to S1 but shorter; may be joined across glabella by shallow furrow. S3 very faintly impressed, very short and directed slightly forwards. S4 very short, shallower than S2, and inclined forwards. Axial furrow of greatest depth between S2 and S3. Preglabellar furrow narrow (sag.). Occipital furrow straight or gently curved posteriorly, deep distally, shallowing adaxially. Occipital ring moderately convex (tr), in lateral profile slopes slightly upwards with pronounced medial node or short spine on posterior margin. Sagittal length of occipital ring approximately one-fifth that of glabella. Palpebral lobes long (exsag.), gently convex (tr.) and weakly sigmoidal in outline, with exsagittal length approximately three-fifths sagittal glabellar length. Palpebral lobes defined by narrow, deep furrow that shallows markedly along the posterior margin of the very short ocular ridge. Anterior border of moderate width, defined either by shallow furrow, or more commonly by change in slope of exoskeleton; separated from glabella by narrow preglabellar field that is strongly upturned. Posterior border narrow adaxially, widening gradually distally, directed gently posterolaterally. Posterior border furrow of greater width (exsag.) than border, moderately deep distally with rapid shallowing adaxially. Course of anterior sections of facial suture divergent with width (tr.) of anterior border less than width between lateral margins of palpebral lobes. Posterior section of facial suture not known. Sculpture on the anterior border is of low terrace lines; glabella with medium granules, and more widely-spaced granules of similar size on fixed cheeks.

Remarks. – This species is particularly characterised by being distinctly narrower between the anterior sections of the facial sutures than between the palpebral lobes. Comparison of the type material with the specimens from North Greenland reveals only minor differences in the morphology. The type cranidia have palpebral lobes that are strongly arcuate with short ocular ridges clearly discernible, whilst weakly sigmoidally-shaped lobes and no pronounced differentiation into ocular ridges characterise the specimens from Freuchen Land. Additionally, the relative width of the palpebral area for the type material is slightly greater, the occipital furrow is less well pronounced, and the granular sculpture slightly coarser but such differences are not sufficient for specific distinction.

Fritz (1972) described Z. stribuccus from one cranidium, concluding it to be close to Z. contracta but differing by having longer ocular ridges (and hence shorter palpebral lobes) and more prominent palpebral furrows. Following examination of the type material of the two forms, no differences in palpebral furrow morphology can be detected. While the holotype of Z. stribuccus does have slightly longer ocular ridges than those of Z. contracta, this feature in a single specimen is not sufficient to justify erection of a new species. Variation in ocular ridge length is known both within the type series of Z. contracta and the material from North Greenland. Z. stribuccus is considered to be a junior synonym of Z. contracta.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Zacanthopsis? sp. A

Fig. 42.5

Figured material. – Pygidium; MGUH 23463 from GGU collection 298547.

Other material. - GGU collection 298547.

Description. – Pygidium small, subrectangular in outline. Prominent axis tapers backwards, joined to posterior border by very short (sag.) median ridge. Axis formed of three rings and terminal piece. Wide (tr.) pleural fields crossed by four pairs of wide pleural furrows which terminate as pits in the border furrow. Border narrow, defined by shallow furrow, five pairs of short marginal spines. Spine length decreases posteriorly.

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Discussion. – The specimens are questionably assigned to Zacanthopsis since five pairs of border spines are present (three or four pairs typify the genus), together with four pairs of pleural furrows (two being common for Zacanthopsis). The short (sag.) axis, wide pleural fields and short marginal spines, however, are reminiscent of Zacanthopsis.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Genus Zacanthoides Walcott, 1888

Type species. – By original designation; *Embolimus spinosa* Rominger, 1887, p. 15, pl. 1, fig. 3 from the Middle Cambrian Stephen Formation, British Columbia.

Zacanthoides? sp. A

Fig. 61.2, 3

Figured material. – Cranidium; MGUH 23464-23465 from GGU collection 301340.

Description. - Glabellar sides slightly concave between SO and S2, anteriorly of S2 gentle forwards expansion, bluntly rounded anterior. Four pairs of glabellar furrows; S1 inclined backwards at approximately 50 degrees to an exsagittal line. S2 shorter, slightly shallower and directed backwards at lower angle. S3 and S4 weakly impressed, directed forwards and reaching to axial furrows. Occipital furrow straight, deepens gradually abaxially. Occipital ring with long, slender median spine, directed gently upwards. Long (exsag.) palpebral lobes, narrow (tr.) and sigmoidal in outline. Lobes strongly convex (tr.) with lateral margins steeply inclined. Exsagittal length about three-fifths sagittal glabellar length. Preglabellar furrow wide (sag.), with preglabellar field that is gently upturned, and distinguished from the anterior border by a subtle change in slope. Preocular cheeks slope moderately downwards in an anterolateral direction, until level with anterior of glabella, then gently upturned. Narrow (exsag.) posterior border defined by narrow and deep furrow. Anterior sections of facial suture strongly convex abaxially; posterior section unknown. Sculpture on all parts of cranidium of medium-sized granules.

Discussion. – The strong divergence of the anterior sections of the facial suture and long, slender, sigmoidallyshaped palpebral lobes without differentiation into ocular ridge are more characteristic of *Zacanthoides* than they are of Zacanthopsis. The assignment is tentative because of a lack of knowledge of the complete posterior border; Zacanthoides typically has distinct, posteriorly-directed spines at the terminations of the posterior border. The generic assignment is also uncertain since only cranidia are at hand.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Genus Stephenaspis Rasetti, 1951

Type species. – By original designation *Stephenaspis bispinosa* Rasetti, 1951, p. 181, pl. 10, figs 1-6.

Diagnosis. – After Palmer (1964: F8). Cephalon has narrow (tr.) anteriorly expanded glabella that reaches to narrow (sag.) anterior border. Narrow (tr.) fixed cheeks. Palpebral lobes long (exsag.) and slender. Posterior area of fixed cheek narrow (exsag.). Pygidium subquadrate in outline, gently convex pleural fields lacking well-defined border. Posterolateral margin with pair of slender posteriorly directed spines.

Stephenaspis? avita Palmer, 1964

Fig. 60.2, 5, 8

1964 *Stephenaspis? avitus* Palmer 1964, p. F8, pl. 3. figs 10-14.

Type material. – Holotype cranidium USNM 144296, Natural History Museum, Smithsonian Institution, Washington D. C., from the Lower Cambrian Saline Valley Formation, 8 km north-east of Gold Point, Esmeralda County, Nevada, U. S. A.

Figured material. – Cranidium; MGUH 23466-23468 from GGU collection 301340.

Other material. - GGU collection 301340.

Description. – Specimens from North Greenland conform to the description given in Palmer (1964, p.F8).

Discussion. – Assignment to *Stephenaspis* can only be tentative because only the cranidia are known; it is the pygidium that is most diagnostic. Palmer (1964) commented that eventual assignment of the pygidium which he referred to "genus and species undetermined 4" to *S*? *avita* would produce a trilobite resembling *Poliella denticulata* Rasetti, 1951. A similar pygidium is associated with the North Greenland material of *S*? *avita* (herein de-

scribed as "corynexochid genus and species undetermined A"). This specimen differs from pygidia of *P. denticulata*, however, on account of its ill-defined border and greater number of border spines. Without further material the generic assignment of both exoskeletal elements remains uncertain.

Occurrence in North Greenland. – Henson.Gletscher Formation, (Figs 8A, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Corynexochid genus and species undetermined A

Fig. 61.1

Figured material. – Pygidium; MGUH 23597 from GGU collection 301340.

Description. – Short (sag.) axis of moderate convexity (tr.), formed of two axial rings that are clearly defined, an ill-defined third and terminal piece. Posterior to second axial ring the axis descends rapidly to the pleural fields, anteriorly axis laterally defined by shallow furrow. Pleural fields gently convex (tr.), crossed by four pairs of pleural furrows that are progressively shallower posteriorly. Interpleural furrows wide (exsag.) and terminating in axial furrow as small pits. Poorly defined border very narrow and flat, bears five pairs a triangular-shaped border denticles.

Remarks. – As discussed above, this pygidium may belong with the cranidia assigned to *Stephenaspis? avita* Palmer, 1964.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Family Oryctocephalidae Beecher, 1897 Subfamily Oryctocarinae Hupé, 1953 Genus *Arthricocephalus* Bergeron, 1899

Synonyms. – Oryctocarella Tomashpolskaya & Karpinskii, 1962. Arthricocephalus (Arthricocephalites) Chien & Lin, 1974.

Type species. – By original designation; *Arthricocephalus chauveaui* Bergeron, 1899 from the Lower Cambrian of north-western Guizhou, south-western China.

Diagnosis. – Glabella subrectangular in outline, reaching to anterior border furrow, four pairs of lateral pits; S1 –
S3 generally connected across sagittal line by shallow furrows. Anterior border very short (sag.). Palpebral lobes situated anteriorly; occipital ring short (sag.) and free cheeks narrow (tr.). Thoracic pleurae without pleural spines. Pygidium semicircular with complete, narrow border. Narrow (tr.) axis of five rings does not reach to posterior border.

Remarks. – Arthricocephalus was described from a small number of specimens collected from Tongren County, Guizhou Province, south-western China, that were presented to J. Bergeron by M. Chauveau. Although the age of the specimens was not known, from the general aspect of their form, Bergeron (1899) thought it to be 'ancient', and probably Cambrian. Cambrian rocks are widely distributed in the Tongren area, and Bergeron's specimens are believed to have been collected from the Balang Formation, north of Tongren (Lane *et al.* 1988).

Saito (1934) described Arthricocephalus? primigenius from the Lower Cambrian of north-western Korea. This material, however, does not belong to Arthricocephalus, as was in fact suggested by Saito (1934: 233), and it is here removed from the genus. From an examination of the illustrations, an assignment to Cheiruroides Kobayashi, 1935 is more applicable.

Rasetti (in Moore 1959: 524) considered Arthricocephalus to be unrecognisable, but it is readily assigned to the Oryctocephalidae even on the basis of the somewhat idealised and restored line-drawing of Arthricocephalus chauveaui of Bergeron (1899, fig. 9).

Arthricocephalus was reported from the Henson Gletscher Formation of Freuchen Land by Blaker (1986), this being the first record of the genus from outside China. Lane *et al.* (1988) described the type material (see Fig. 62), and it is this work that has enabled the present revision of the genus.

Arthricocephalus (Arthricocephalites) was erected by Chien & Lin (1974) and, in the opinion of Zhang Wen-Tang (written communication 1986), it differs from Arthricocephalus sensu stricto in longer (exsag.) palpebral lobes, narrower (tr.) fixed cheeks and more obliquely directed ocular ridges. All three characters are very susceptible to individual variability, and it has not been possible to determine any consistent differences from specimens of Arthricocephalus. Arthricocephalus (Arthricocephalites) is therefore considered to be a synonym of Arthricocephalus.

Ju (1983) described Arthricocephalus (Euarthricocephalites) from the upper Lower Cambrian Dachenling Formation of Zhejiang, China, to include the type species A. (E.) laterilobatus and a second species A. (E.) sanxi-kouensis. The illustrations of both are poor and precise detail is not easily determined. Only a single partial cranidium was figured of A. (E.) sanxikouensis, and this does not appear to differ in any way from the illustrated cranidia of A. (E.) laterilobatus; it is possible that they are synonymous. Ju (1983) concluded the subgenus differed from Arthricocephalus sensu stricto in a broader (tr.) gla-

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bella and by L1 being transversely trilobed. In this latter character the specimens are unique, and enable distinction at the specific level. The subgenus is questioned, however, in view of the poor preservation of the type material, and since it appears to differ only in this one character.

It has previously been suggested that the monospecific *Oryctocarella* Tomashpolskaya & Karpinskii, 1962 is a synonym of *Arthricocephalus* (Suvorova 1964: 235; Shergold 1969: 40). These comparisons were based on the line-drawing of *A. chauveaui* given by Bergeron (1899, fig. 9) which, although somewhat idealised, is an accurate representation. Following examination of the type series of *A. chauveaui*, the status of *Oryctocarella* can now be assessed. The holotype of *Oryctocarella sibirica* (Tomashpolskaya in Khalfin 1960) is a complete specimen comparable in all morphological features to *A. chauveaui*, and the two are considered to be synonymous.

The classification of Arthricocephalus, and indeed of all the oryctocephalids, is at present in some confusion. Following the detailed work of Chernysheva (1962), both Suvorova (1964) and Shergold (1969) agreed on the assignment of Arthricocephalus to the subfamily Oryctocarinae Hupé, 1953, and this was the system of classification followed by Zhang (1980b). However, Zhang et al. (1980) introduced without discussion a new classification which split the genera previously included in the subfamily Oryctocarinae into three subfamilies (a restricted Oryctocarinae and two new subfamilies) all of which were assigned to the Feilongshaniidae. Arthricocephalus was assigned to the subfamily Feilongshaniinae. The diagnosis of this subfamily is very general and does not enable distinction from the subfamily Oryctocarinae. In the absence of a detailed account of the basis for the classification proposed by Zhang et al. (1980), the classification proposed by Suvorova (1964) is followed herein.

Whittington (1995), in a recent review of North American oryctocephalids exclusive of the Greenland forms described herein, recognised two subfamilies, Oryctocephalinae and Oryctocarinae.

Arthricocephalus chauveaui Bergeron, 1899

Figs 62; 63; 64.1-4

- 1899 Arthricocephalus chauveaui n. sp. Bergeron, p. 514, fig. 9.
- 1960 Oryctocara sibirica Tomashpolskaya sp. nov., in Khalfin, p. 199, pl. 33, fig. 5.
- 1961 Arthricocephalus duyunenesis Chien (sp. nov.), p. 97, pl. 1, figs 19-20, pl. 2, figs 5-10.
- 1962 Oryctocarella sibirica gen. et. sp. nov., Tomashpolskaya & Karpinskii, p. 156, pl. 1, figs 1-6.
- 1962 Oryctocara (Ovatoryctocara) granulata Chernysheva, sp. nov., p. 40, pl. 5, figs 6-8.



Fig. 62. *Arthricocephalus chauveaui* Bergeron, 1899. Balang Formation (Lower Cambrian), north of Tongren, north-eastern Guizhou, south-western China, x 12. 1, lectotype, disarticulated specimen, dorsal view of thorax and pygidium, ventral view of cranidium and hypostome, EM 90001b, l'Université Claude Bernard, Lyon, France. 2, paralectotypes, complete specimens, dorsal view. 3, paralectotype, thorax, dorsal view.

- 1965 Arthricocephalus chauveaui Bergeron; Lu et al., p. 64, pl. 7, figs 7a-c.
- 1965 Arthricocephalus Bergeron, Lu et al.; p. 26, pl. 1, fig. 5.
- 1965 Arthricocephalus duyunensis Chien; Lu et al., p. 108, pl. 17, figs 2-5.
- 1969 *Neopagetina nomokonovi* Semashko sp. nov., p. 72, pl. 1, fig. 13, (*non* pl. 1, figs 11-12).
- 1971 Oryctocara (Ovatoryctocara) sp., Chernysheva, p. 140, pl. 13, figs 8-9.
- 1974 Arthricocephalus duyunensis Chien; Lu et al., p. 95, pl. 36, fig. 9.
- 1977 Arthricocephalus chauveaui Bergeron; Zhou et al., p. 130, pl. 42, fig. 3.
- 1977 Arthricocephalus granulus Qian et Lin (MS), in Zhou et al., p. 130, pl. 42, figs 1-2.
- 1980 Arthricocephalus chauveaui; Zhang et al., p. 275, pl. 92, figs 1-2.
- 1980 Arthrococephalus [sic] horridus Qian et Lin (sp. nov.), in Zhang et al., p. 275, pl. 92, figs 7-9.
- 1980 Arthricocephalus (Arthricocephalites) granulus

Chien et Lin, 7; in Zhang *et al.*, p. 277, pl. 90, fig. 8, pl. 93, fig. 4, pl. 94, figs 1-2.

- 1983 Arthricocephalus (Arthricocephalites) granulus Chien et Lin; Ju, p. 632, pl. 2, figs 12-13.
- 1983 Arthricocephalus (Arthricocephalites) sp., Ju, p. 632, pl. 2, figs 14-15.
- 1983 Arthricocephalus fuyangensis sp. nov., Ju, p. 632, pl. 2, fig. 16.
- 1985 Arthricocephalus duyunensis Chien; Zhang & Zhou, p. 263, pl. 2, figs 8-9.
- 1985 Arthricocephalus tenuis sp. nov., Zhang & Zhou, p. 263, pl. 2, figs 10-12.
- 1985 Arthricocephalus (Arthricocephalites) cf. granulus Chien et Lin; Zhang & Zhou, p. 264, pl. 2, fig. 13.
- 1985 Arthricocephalus sp., Zhang & Zhou, p. 264, pl. 2, fig. 14.
- 1986 Arthricocephalus duyunensis Chien, 1961; Blaker, p. 68.
- 1988 Arthricocephalus chauveaui Bergeron, 1899; Lane et al., p. 555, pl. 1, figs 1-6.

1995 Arthricocephalus chauveaui Bergeron, 1899; Whittington, p. 555.

Type material. – Lectotype cranidium (EM 90001b) from the Lower Cambrian of north-eastern Guizhou, southwestern China. The type material is housed in the Geology Department, l'Université Claude Bernard, Lyon, France.

Figured material. – Complete specimen; MGUH 18.225 from GGU collection 315095. Cranidium; MGUH 23469-23472 from GGU collection 315095, MGUH 23473 from GGU collection 315096. Pygidium; MGUH 23474 from GGU collection 315099.

Other material. - GGU collections 271750 and 315095.

Diagnosis. – After Lane *et al.* (1988). Thorax of eight segments with minimal decrease in width (tr.) posteriorly. Axis narrow, about one-sixth total width. Pygidial axis about two-thirds sagittal pygidial length; five pairs of pleural furrows. Sculpture of closely-spaced coarse granules on fixed cheeks, more scattered on glabella. Thorax and pygidial axis with subdued granules, pleural areas with small to medium, closely-spaced granules.

Description. - Cranidium gently convex (tr. & sag.) with elongate, subrectangular glabella. Lateral margins diverge slightly forwards or are subparallel; anterior very gently rounded, reaching to anterior border furrow. Glabella gently convex (tr), defined laterally by narrow axial furrows. Four pairs of deep glabellar pits; all of about equal depth. S4 rarely connected to axial furrow and never joined across glabella. S1 - S3 of more variable morphology, frequently connected across glabella by shallow furrow, and occasionally isolated from the axial furrows. Depth of transverse furrows greatest on immature cranidia. In some specimens a shallow longitudinal furrow connects S2 and S3, and more rarely S1. Occipital furrow (SO) formed distally by deep pits which are connected by a shallow, narrow furrow. Occipital ring gently convex (tr.), short (sag.) with low median node. Sagittal length approximately one-ninth that of glabella. Anterior border very short (sag), widening slightly abaxially, gently curved with slight forwards deflection in front of glabella. Anterior border defined by narrow furrow of moderate depth, with reduction in both width and depth in front of glabella. Broad (tr.) palpebral areas of gentle transverse convexity. Width (tr.) about equal to, or slightly greater than, basal glabellar width. Short (exsag.) palpebral lobes situate anteriorly, centred at about midlength of L3. Short ocular ridges of moderate relief, gently curved and positioned close to the anterior border furrow. Posterior areas of fixed cheek very wide (tr.); approximately twice width across base of glabella. Posterior border narrow close to axial furrow, widening distally with rounded terminations. Border furrow weakly sigmoidal in outline, wide (exsag.) and of moderate depth distally, shallowing adaxially. Course of anterior sections of facial suture convergent forwards in gentle curve. Posterior sections initially very strongly divergent, then strongly curved posteriorly over border.

Width (tr.) of thorax decreases minimally backwards from the anterior segment; axial rings moderately convex (tr.). Relative width of axial ring approximately one-sixth that of segment. Axis defined by shallow furrows. Wide (tr.) pleurae with slight geniculation at about one-half width, and rounded tips. Pleura with prominent, narrow, deep pleural furrow.

Pygidium semicircular in outline, with short (sag.) axis that terminates well in front of posterior margin. Sagittal length of axis about two-thirds that of pygidium. Axis gently convex (tr.) and tapering markedly backwards, formed of five complete rings. Axial furrow narrow and deep, continuous around posterior of axis. Connective band slightly inflated. Inter-ring furrows straight and of moderate depth. Pleural regions crossed by five pairs of narrow pleural furrows. Interpleural furrows considerably narrower and shallower. Wirelike convex border defined by very narrow, shallow furrow.

Sculpture of the cranidium consists of closely-spaced granules on the fixed cheeks, whilst the glabella has scattered medium sized granules. Granule size on the fixed cheeks is variable, although coarse ones dominate. Not-



Fig. 63. Arthricocephalus chauveaui Bergeron, 1899. Henson Gletscher Formation. 1, cranidium and thoracic segment, dorsal view, MGUH 23471, x 19. 2, cranidium, partially exfoliated, dorsal view, MGUH 23469, x 14. 3, cranidium, internal mould, dorsal view, MGUH 23470, x 16. All from GGU collection 315095.

ably the posterior border tends to have a higher proportion of medium to small-sized granules. The thoracic axis has rather subdued granular sculpture, whilst the pleurae have more widely-spaced and smaller granules than those on the cranidial fixed cheeks. Granules are rare and have an irregular distribution on the pygidial axis whilst the pleural regions are sculptured with medium and small granules that are particularly concentrated at the pleural tips, and elsewhere are of moderate density.

Discussion. – This material was reported by Blaker (1986) as *A. duyunensis* Chien, 1961 but this assignment is revised following examination of the type series of *A. chauveaui*.

Blaker (1986: 68) concluded that the palaeogeographic reconstruction for the Cambrian given by Scotese et al. (1979; see also Scotese & McKerrow 1990), which places Greenland and China in close proximity and at similar latitudes, gave a more feasible explanation of the distribution of the Arthricocephalus in China and Greenland than the reconstruction of Morel & Irving (1978). From this reconstruction, it would be expected to find Arthricocephalus in Siberia. At that time, no record had been traced from Siberia, but the present synonymisation of Oryctocarella with Arthricocephalus provides this record. In addition, the following Siberian forms are recognised as synonyms of A. chauveaui; Oryctocara (Ovatoryctocara) granulata Chernysheva, 1962, Oryctocara (Ovatoryctocara) sp. described by Chernysheva (1971) and a pygidium assigned to Neopagetina nomokonovi sp. nov. by Semashko (1969, pl. 1, fig. 13) from a Middle Cambrian sandstone-shale sequence in the Batenevsky Mountain Range, Siberia.

Specimens subsequently assigned to O.(Ov.) granulata Chernysheva, 1962 in Egorova et al. (1976) and Savitsky et al. (1972) are not synonyms of the type species. These specimens are discussed below under the genus Oryctocara Walcott, 1908.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Genus Haliplanktos gen. nov.

Derivation of name. – From the Greek *haliplanktos*, a 'wanderer in the sea'.

Type species. – *Haliplanktos jishouensis* (Zhou in Zhou *et al.* 1977) from the Lower Cambrian of southern China.

Diagnosis. – Oryctocephalid with broad (tr.) glabella strongly expanded anterior to S3; sides concave between SO and S3. Four pairs glabellar furrows, S4 isolated, S1 – S3 joined across glabella. Palpebral lobes centred at midlength of L3. Wide (tr.) posterior areas of fixed cheek. Very narrow (tr.) free cheeks. Thorax of six segments, all of about equal width (tr.); deep and wide pleural furrows. Pleurae with rounded terminations. Semicircular pygidium, narrow (tr.) axis not reaching pygidial margin. Pleural regions crossed by six pairs of deep, narrow pleural furrows; narrow, shallow interpleural furrows. Pygidial border narrow and poorly defined, narrowest posteriorly. No apparent sculpture.

Remarks. – Haliplanktos differs from Arthricocephalus in the strong expansion of the glabella anterior to S3, the well defined lateral division of the glabella, a thorax of six segments and a pygidium with an ill-defined, rather flat border and pleural fields crossed by six pairs of deep pleural furrows.

Haliplanktos jishouensis (Zhou in Zhou et al. 1977)

Fig. 64.5-7

- 1963 Arthricocephalus chauveaui Bergeron, 1899, Egorova et al., p. 20, pl. 2, fig. 9.
- 1965 Arthricocephalus chauveaui Bergeron, Lu et al., p. 108, pl. 17, fig. 1.
- 1977 Arthricocephalus (Arthricocephalites) jishouensis Zhou (sp. nov.), in Zhou et al., p. 131, pl. 42, figs 4-6.
- 1980 Arthricocephalus (Arthricocephalus) pulchellus Zhang et Qian (sp. nov.), in Zhang et al., p. 276, pl. 92, fig. 3.
- 1986 Arthricocephalus jishouensis Zhou, 1977; Blaker, p. 68.

Diagnosis. – As for genus.

Type material. – Figured by Zhou *et al.* (1977, pl. 42, figs 4-6). Specimen numbers are IV 70026-28 but the collection locality and repository are not known.

Figured material. – Complete specimen; MGUH 23475 from GGU collection 315096, MGUH 23476 from GGU collection 315099. Cranidium; MGUH 23477 from GGU collection 315095.

Other material. - GGU collection 315095.

Description. – Cephalon semicircular in outline with gently convex (tr. & sag.) elongate glabella. Glabellar sides gently concave between SO and S3, anteriorly of S3 expanded rapidly forwards with rounded anterior reaching to the anterior border furrow. Four pairs of glabellar furrows; S1 - S3 all of similar form, being short, deep and transverse and reaching the axial furrow; connected across the glabella by shallower transglabellar furrows. S4 formed of deep, isolated pits. S1 - S3 define three distinct lobes, with L1 and L3 being of about equal



Fig. 64. Trilobites from the Henson Gletscher Formation. 1-4. Arthricocephalus chauveaui Bergeron, 1899. 1, cranidium, internal mould, dorsal view, MGUH 23473 from GGU collection 315096, x 16. 2, complete specimen, meraspid degree 7, dorsal view, MGUH 18.225 from GGU collection 315095, x 8. 3, cranidium, partially exfoliated, dorsal view, MGUH 23472 from GGU collection 315095, x 19. 4, meraspid pygidium, dorsal view, MGUH 23474 from GGU collection 315099, x 11.

5-7. *Haliplanktos jishouensis* (Zhou, 1977). 5a-c, complete specimen, holaspid, dorsal view, MGUH 23476 from GGU collection 315099, x 7, x 16 and x 13, respectively. 6, damaged cranidium, internal mould, MGUH 23477 from GGU collection 315095, x 12. 7, damaged complete specimen, holaspid, partially exfoliated, MGUH 23475 from GGU collection 315096, x 9.

sagittal length, and L2 of slightly greater length. Occipital furrow (SO) formed distally of short, deep incisions joined across the axial line by a shallower transverse furrow. Occipital ring gently convex (tr. & sag.) with almost straight posterior margin. Sagittal length of ring approximately one-ninth that of glabella. Anterior border and furrow very narrow (sag.) in front of glabella, widening abaxially. Width (tr.) of convex palpebral areas about three-quarters that of glabella across base. Gently curved palpebral lobes, exsagittal length approximately one-quarter sagittal glabellar length. Lobes positioned anteriorly, with midpoints being on a line that passes through the midlength of L3. Ocular ridges short, low and gently curved. Defined by shallow furrow and positioned close to the anterior border furrow. Posterior area of fixed cheek wide (tr.). Posterior border widest distally, narrowing adaxially; straight posterior margin, point of geniculation at about midlength, terminations rounded. Posterior border furrow of medium width (exsag.) and depth, directed anterolaterally. Course of anterior sections of facial suture short, convergent forwards in gentle curve. Posterior sections of suture strongly divergent to posterior border furrow, then turned strongly posteriorly over border.

Free cheeks with very narrow (tr.) ocular platform, and a lateral border that is well defined anteriorly by a deep furrow, posteriorly by a change in exoskeletal slope.

Thorax of six segments of about constant transverse width, whilst the axis tapers backwards. Axial rings moderately convex (tr.), axis defined laterally by narrow, deep furrows. Pleurae with geniculation at about midwidth, rounded terminations and deep pleural furrows that narrow distally.

Pygidium with maximum transverse width about twice sagittal length. Narrow (tr.) axis composed of six rings, decreases in width posteriorly, not reaching the pygidial margin. Sagittal length of axis approximately three-quarters that of pygidium, laterally defined by deep furrow that is continuous around the posterior. Pleural regions moderately convex (tr.), crossed by six pairs of narrow and deep pleural furrows that reach to the border furrow. Pygidial border poorly-defined and narrow, with a slight increase in width anterolaterally.

Exoskeleton without apparent sculpture.

Remarks. – Blaker (1986) previously referred this material to Arthricocephalus jishouensis (Zhou in Zhou et al. 1977). This assignment is now revised following examination of the type material of Arthricocephalus and the specimens are placed in a new genus, Haliplanktos.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Genus Ovatoryctocara Chernysheva, 1962

Type species. – By original designation; *Oryctocara ovata* Chernysheva, 1960 from Middle Cambrian strata in the basin of the River Anabar, Malaya Kuonauka, Ydzha, central part of the North Siberian Platform.

Remarks. – The type and other material of *Oryctocara* geikei were described by Whittington (1995), and *Ovato-ryctocara* was regarded as a distinct genus, not as a subgenus of *Oryctocara* as originally proposed by Chernysheva in 1962.

Ovatoryctocara sp. A

Figs 65; 66; 67.5

- 1972 O. (Ov.) granulata Chernysheva, in Savitsky et al., p. 77, pl. 16, fig. 10.
- 1976 O. (Ov.) granulata Chernysheva, in Egorova et al., p. 96, pl. 43, figs 15-17.



Fig. 65. *Ovatoryctocara* sp. A. Henson Gletscher Formation. 1, pygidium, dorsal view, MGUH 23483 from GGU collection 271485, x 14. 2, damaged pygidium, dorsal view, MGUH 23484 from GGU collection 271485, x 13. 3, pygidium, dorsal view, MGUH 23481 from GGU collection 218610, x 22.



Fig. 66. *Ovatoryctocara* sp. A. Henson Gletscher Formation. 1, pygidium, internal mould, dorsal view, MGUH 23480, x 24. 2, cranidium, internal mould, dorsal view, MGUH 23479, x 24. All from GGU collection 218610.

Figured material. – Cranidium; MGUH 23478-23479 from GGU collection 218610. Pygidium; MGUH 23480-23482 from GGU collection 218610, MGUH 23483-23484 from GGU 271485. Free Cheek; MGUH 23485-23486 from GGU collection 218610 (Fig. 67.4, 9 as oryctocephalid free cheek).

Other material. - GGU collections 218610, 271485.

Description. – The cranidium is similar to that of *Arthricocephalus chauveaui* Bergeron, 1899 except that the glabella expands weakly anteriorly and glabellar furrow development differs. For the smallest cranidia, S1 - S3 are formed of small pits adjacent to the axial furrows, and connected across the glabella by very shallow, wide (sag.) furrows; S4 being poorly-defined. For larger cranida S4 is formed of shallow pits connected to the axial furrows; S1 - S3 are of distinctive keyhole morphology, reaching to the axial furrows but not joined across glabella.

Pygidium subi-elliptical in outline, gently convex (tr. & sag.). Axis tapers moderately backwards, not reaching pygidial margin. Sagittal length of connective band approximately one-fifth that of pygidium. Axis formed of nine rings with inter-ring furrows weakly impressed except distally. Pleural regions crossed by between seven and nine pairs of deep and narrow pleural furrows that reach nearly to the pygidial margin. Interpleural furrows very narrow.

Sculpture of the cranidium consists of coarse, closelyspaced granules on the fixed cheeks whilst the glabella is unsculptured. Lateral border of free cheek with coarse granules, some of which are perforate. Genal spine and ocular platform without apparent sculpture. Pygidial axis with scattered coarse granules; closely-spaced, medium and coarse granules on pleural regions.

Discussion. – The type material of *Oryctocara (Ovato-ryctocara) granulata* Chernysheva, 1962 is considered to be synonymous with *Arthricocephalus chauveaui* Bergeron, 1899. Material subsequently assigned to *O. (Ov.) granulata* is considered to be conspecific with the speci-

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mens from North Greenland here assigned to *Ov.* sp. A. *Oryctocara granulata* was recorded from eastern Newfoundland by Landing (1992 and references therein; Zhuravlev 1995) but the material has not been figured.

Two possible oryctocephalid free cheeks are also figured here. The free cheek has an ocular platform slightly wider (tr.) than that of the lateral border at the midpoint of palpebral lobe. The ocular platform is gently convex and distinguished from the border by a slight change in exoskeletal slope. The lateral margin is gently curved and confluent with a long, slender genal spine.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 9, localities 2 and 5). Age: Early Cambrian, *Olenellus* Zone.

Genus Oryctocephalus Walcott, 1916

Synonym. – Oryctocephalus (Vinakainella) Rusconi, 1952 (after Poulsen 1958b).

Type species. – By original designation; *Oryctocephalus primus* Walcott, 1886, Middle Cambrian, from the Pioche Formation, Pioche, Nevada, U. S. A.

Remarks. – Chernysheva (1962) synonymised Oryctocephalina Lermontova, 1940 with Oryctocephalus following Rasetti (in Moore 1959: 220). Kobayashi (1961: 224) maintained Oryctocephalina and subsequently both Suvorova (1964: 234) and Shergold (1969: 47) considered the genus to be valid. At present the pygidium of Oryctocephalina is only known for the Australian O. lancastroides Shergold, 1969, and it is upon this species that Shergold's opinion was based.

Whittington (1995: 546) redefined Oryctocephalus, largely on the basis of the only completely-known specimen from the Middle Cambrian, and discussed the difficulties in using the generic names Oryctocephalites and Oryctocephalina. The species described below is referred to Oryctocephalus, but the oval outline of the glabella (the maximum width in many cranidia lying between S2 and S3) suggests that it might equally be regarded as a species of *Oryctocephalites*.

Oryctocephalus vicinus Chernysheva, 1962

Figs. 67.1-3, 6-8, 10; 68

1962 Oryctocephalus vicinus Chernysheva, sp. nov., p. 19, pl. 2, figs 9, 10.

Type material. – Holotype cranidium (N. E. Chernysheva collection 10/8194) is from Middle Cambrian strata, basin of the River Orlyonok, Siberia. The type material is deposited in the Central Siberian Geological Museum, Novosibirsk, Russia.

Figured material. – Cranidium; MGUH 23487-23495 from GGU 218610. Free cheek; MGUH 23496-23497 from GGU collection 218610. Hypostome; MGUH 23498 from GGU collection 218610.

Other material. – GGU collections 218610 (abundant), 225709, 225714, 271483, 271485, 271750, 298545, 298553, 301340, 301349, 315097.

Description. - Cranidium subquadrate in outline, width between anterior sections of facial sutures approximately three-quarters width between tips of posterior border. Glabella broad (tr.) and elongate, gently convex (tr. & sag.), defined laterally by narrow axial furrows that shallow posteriorly of S1. Anterior of glabella almost straight, reaching to anterior border furrow. Glabellar sides subparallel or gently adaxially concave between SO and S1, at level of S1 glabella expands forwards until level of S2, between S2 and S3 more gentle expansion or rarely subparallel. Four pairs of glabellar furrows; SO gently concave posteriorly, distally formed of deep pits. S1 - S3 represented by deep pits commonly isolated from the axial furrows, although occasionally connected by shallow transverse furrows. S1 joined across glabella by narrow furrow of variable depth. S4 slot-like, short, shallow, usually transverse and reaching to axial furrow. Occasionally very shallow, longitudinal furrows connect S1 and S2, and rarely extended to join S2 and S3. Occipital ring gently convex (tr. & sag.), sagittal length about oneseventh that of glabella. Anterior border gently convex, narrowest in front of glabella, anterior margin deflected around front of glabella. Border furrow deep and narrow in front of glabella, widening and considerably shallower distally. Palpebral areas wide (tr.) and very gently convex. Long (exsag.) palpebral lobes, wide and strongly convex (tr.), very slightly curved. Lobes centred at about midlength of L2, defined by narrow furrow which is continuous with furrow defining posterior margin of pronounced ocular ridges. Ocular ridges sometimes divided by shallow intraocular furrow positioned towards the anterior margin. Posterior border narrow abaxially, widening distally, directed gently posterolaterally terminating in small posteriorly-directed spines. Posterior border furrow straight or faintly sigmoidal in outline. Anterior sections of facial suture short, slightly convergent in very gentle abaxially convex curve. Posterior sections short, gently curved and divergent.

Free cheek with very narrow (tr.) crescentic ocular platform separated from border by furrow of moderate depth and width. Lateral margin very slightly curved; border continuous with long (exsag.), slender, posterolaterally-directed spine.

Rostral-hypostomal plate (Fig. 67.10) like that of *Oryctocephalus oepiki* (Shergold 1969, pl. 1, fig. 4; pl. 2, fig. 4) and that of *O. reynoldsi* (Whittington 1995, pl. 1, figs 3, 4, 6); gently convex (tr. & sag.). Lateral margins subparallel, posterior margin strongly rounded (see discussion below).

On small specimens sculpture of the palpebral area is of low, widely-spaced granules. All other parts without apparent sculpture.

Discussion. – The hypostome figured herein bears a strong overall resemblance to that of *Oryctocephalus oepiki* Shergold. 1969.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 9, localities 2 and 5). Age: Early Cambrian, *Olenellus* Zone.

Subfamily Lancastriinae Kobayashi, 1935

Remarks. – There has been no general agreement amongst authors (Chernysheva 1962; Suvorova 1964; Shergold 1969) concerning the generic composition of this subfamily. It was not used by Whittington (1995).

Genus Lancastria Kobayashi, 1935

Synonyms. – Changaspis Chien, 1961, Pseudolancastria Lee in Egorova et al. 1963 (after Zhang 1980b), Chienaspis Suvorova, 1964 were regarded as synonyms by Zhang (1989). Paraoryctocephalops Tomashpolskaya in Khalfin 1960 and Goldfieldia Palmer, 1964 are here also placed in synonymy.

Type species. – By original designation; *Olenopsis roddyi* Walcott, 1912 from the Lower Cambrian of Lancaster County, Pennsylvania, U. S. A. (cf. Whittington 1995).



Fig. 67. Trilobites from the Henson Gletscher Formation.

1-3, 6-8, 10. *Cryctocephalus vicinus* Chernysheva, 1962. 1, cranidium, partially exfoliated, dorsal view, MGUH 23495, x 8. 2, free cheek, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23491, x 17. 6, damaged cranidium, partially exfoliated, dorsal view, MGUH 23491, x 17. 6, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 17. 6, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23497, x 15. 3, damaged cranidium, partially exfoliated, dorsal vie sal view, MGUH 23493, x 16. 8, damaged cranidium, partially exfoliated, dorsal view, MGUH 23489, x 13. 10, hypostome, partially exfoliated, ventral view, MGUH 23498, x 16. All from GGU collection 218610.

11. Lancastria? sp. A. 11, pygidium, dorsal view, MGUH 23499 from GGU collection 218610, x 36.

5. Ovatoryctocara sp. A. 5, damaged pygidium, dorsal view, MGUH 23482 from GGU collection 218610, x 14.5.

4, 9. Oryctocephalid free cheek (see Ovatoryctocara sp. A). 4, damaged free cheek, dorsal view, MGUH 23486, x 7.5. 9, free cheek; partially exfoliated, dorsal view, MGUH 23485, x 9.5. Both from GGU collection 218610.



Fig. 68. *Oryctocephalus vicinus* Chernysheva, 1962. Henson Gletscher Formation. 1, cranidium, internal mould, dorsal view, MGUH 23494, x 9.5. 2, cranidium, partially exfoliated, dorsal view, MGUH 23492, x 13. 3, damaged free cheek, dorsal view, MGUH 23496, x 15. 4, cranidium, partially exfoliated, dorsal view, MGUH 23490, x 12.5. 5, cranidium, partially exfoliated, dorsal view, MGUH 23497, x 18. All from GGU collection 218610.

Lancastria plana (Tomashpolskaya in Khalfin 1960)

Figs 69; 70; 71.1, 3-5, 7, 8; 72.2

- 1960 Paraoryctocephalops plana Tomashpolskaya in Khalfin, p. 200, pl. 23, fig. 6.
- 1962 Paraoryctocephalops plana Tomashpolskaya; Tomashpolskaya & Karpinskii, p. 158, pl. 1, figs 7-9.
 1986 Changaspis sp. nov., Blaker, p. 68.

Type material. – Holotype cranidium, specimen number 863(3)/58 held at the Geological Museum of the Tomsk Technical Institute, Tomsk, USSR. The type series is from the Batenevsky Kryazh region of the Dolgiy Mys mountain range, western Siberia.

Figured material. – Complete specimen; MGUH 23500 from GGU collection 315095. Hypostome, thorax and pygidium; MGUH 23501-23502 from GGU collection 301341. Partial thorax and pygidium; MGUH 23503 from GGU collection 225707, MGUH 23504 from GGU collection 315095. Cranidium; MGUH 23505-23508 from GGU collection 271485. MGUH 23509 from GGU 315095, MGUH 23510-23511 from GGU collection 301341.

Other material. – GGU collections 271485 (abundant), 301341, 315095 (abundant), 315096 and 315107.

Diagnosis. – Oryctocephalid with elongate glabella. Four pairs glabellar furrows, S1 frequently connected across glabella. Longitudinal furrow may connect S2 and S3. Sagittal depression in glabellar anterior. Wire-like anterior ridge. Thoracopygon of 15 segments. Pleurae extend into long, spines.

Description. - Cephalon semicircular in outline, gently convex (tr. & sag.). Cranidium subquadrate in outline with elongate glabella and narrow, moderately deep axial furrows. Anterior of glabella almost straight, occasionally poorly defined. Glabellar sides subparallel between SO and S1, at level of S1 rapid anterior expansion. Four pairs of glabellar furrows of variable morphology. SI short, arcuate, moderately deep and directed gently backwards, occasionally isolated from axial furrows. S1 frequently connected across glabella by narrow, gently curved furrow of variable depth. S2 straight or gently curved, transverse or directed weakly backwards, of similar depth and length to S1; isolated from axial furrows and not joined across glabella. S3 gently arcuate, commonly reaching to axial furrows but isolated across glabella. S4 short, shallow and transverse. S1 - S3 may be of pit-like morphology. On some cranidia a longitudinal furrow connects the deepest parts of S2 and S3, and is also known to continue across L2 to S1. SO straight or gently concave posteriorly, deepest distally, shallowing over axial line. Occipital ring gently convex (tr. & sag.), with

Fig. 69. Lancastria plana (Tomashpolskaya, 1960). Henson Gletscher Formation. 1, damaged cranidium, partially exfoliated, dorsal view, MGUH 23511 from GGU collection 301341, x 8.5. 2, damaged cranidium, dorsal view, MGUH 23510 from GGU collection 301341, x 4. 3, damaged cranidium, partially exfoliated, dorsal view, MGUH 23506 from GGU collection 271485, x 8. 4, damaged cranidium, partially exfoliated, dorsal view, MGUH 23507 from GGU collection 271485, x 9.



centrally positioned, low node and a sagittal length that is about one-sixth that of glabella. Weakly developed sagittal depression in anterior glabellar lobe of most specimens. Cranidia with a poorly defined glabellar front possess a more pronounced depression. Anterior margin of cephalon variable from straight to moderately curved with wire-like anterior ridge defined by change in exoskeletal slope. Palpebral areas wide and gently convex (tr.). Transverse width about equal to, or slightly greater than, basal glabellar width. Palpebral lobes poorly preserved on most specimens, where known moderately long (exsag.), wide (tr.) and gently curved. Lobes centred at approximately midpoint of L2. Ocular ridges pronounced, very gently curved and slightly narrower than palpebral lobes. Furrow defining anterior margin of ocular ridge merges with anterior border furrow. Posterior



Fig. 70. Lancastria plana (Tomashpolskaya, 1960). Henson Gletscher Formation. Damaged cranidium dorsal view, MGUH 23505 from GGU collection 271485, x 8.

border with gradual increase in width (exsag.) distally, terminating in short, posterolaterally-directed spines. Anterior sections of facial suture gently curved with overall slight convergence. Posterior sections short and strongly divergent.

Free cheek of maximum transverse width slightly less than basal glabellar width. Ridge inside lateral border extends backwards to approximately the level of the posterior border furrow. Genal spines short, stout and directed posterolaterally.

Rostral-hypostomal plate (Figs 71.5; 72.2) like that of the type species, *L. roddyi* and *L. lancastroides* (Shergold, 1969), the rostral portion bounded by an outwardlydirected connective suture and wider (tr.) than the hypostomal portion. The latter with narrow lateral and posterior borders, the convex middle body divided into a larger anterior lobe and a smaller, crescentic lobe.

Thoracopygon formed of fifteen segments. Thorax tapers gently backwards over the anterior six segments, then more rapidly posteriorly. Moderately convex (tr.) axial rings with transverse width between one-quarter and one-third that of segment. Inter-ring furrows narrow (sag.) and deep, terminating laterally in deep pits. Axis defined laterally by narrow furrows. Each pleura has a narrow (exsag.) furrow that shallows adaxially, and is gently sigmoidal in outline. Pleurae extend into long, posterolaterally directed spines which are directed progressively more strongly backwards, such that the posterior two pairs almost join at their distal ends along the sagittal line. Whittington (1995: 554) remarked on the difficulty in detecting the boundary between the thorax and the pygidium in the type species; the present material suggests that there may be up to twelve thoracic segments (Figs 71.3, 5, 7; 72.2).

No part of the exoskeleton has noticeable sculpture.

Discussion. – Paraoryctocephalops Tomashpolskaya in Khalfin 1960 is a monospecific genus described from earliest Middle Cambrian strata on the Bateneviskiy spur of the Kuzetskiy Ridge, western Siberia. The holo-

type cranidium and two paratype cranidia were figured by Tomashpolskaya & Karpinskii (1962, pl. 1, figs 7-9). The morphology of these specimens falls within the range known from the North Greenland material, and



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Fig. 72. Trilobites from the Henson Gletscher Formation.

1, 3, 4. *Ptychoparella* sp. A. 1a, b, cranidium, partially exfoliated, lateral and dorsal views, MGUH 23548, x 12. 3, cranidium, partially exfoliated, dorsal view, MGUH 23549, x 9.5. 4, cranidium, partially exfoliated, dorsal view, MGUH 23550, x 11. All from GGU collection 225709.

2. Lancastria plana (Tomashpolskaya, 1960) Hypostome and thorax, ventral view, MGUH 23501 from GGU collection 301341, x 6.

accordingly the genus is synonymised with Lancastria.

Palmer (1964: F7) described *Goldfieldia*, with type species *G. pacifica*, from Lower Cambrian strata of the Saline Valley Formation, Esmeralda County, Nevada, U. S. A. Subsequently, a second species, *G. ninguis* Palmer, 1968 was described from early Middle Cambrian strata of Antarctica and considered to be "... remarkably similar to the type species." The principal differences cited for *G. ninguis* were the more slot-like glabellar furrows, and marginally shorter palpebral lobes and posterior area of the fixigenae. Differences in glabellar furrow morphology are not uncommon within an oryctocephalid species, whilst the reported differences in proportions are not substantiated from study of the type specimens of both species. *G. ninguis* is placed in synonomy with *G. pacifica*.

Goldfieldia was recorded from the Lower Cambrian of Kunshan County, Jiangsu Province, China, by Zhang & Zhou (1985). They described a fauna containing three species of Arthricocephalus, a new species of Changaspis, a new Goldfieldia species and the new genus Kunshanaspis. Only a single cranidium of Goldfieldia kunshanaspis Zhang & Zhou, 1985 was illustrated; this is very similar to the holotype of G. pacifica figured by Palmer (1964), and is possibly conspecific. Goldfieldia is known only from cranidia, and these are characterised by a glabella that is poorly-defined anteriorly, narrowest (tr.) at the occipital ring, a frontal lobe with a median depression in the anterior part and a wire-like anterior rim. The specimens of Lancastria plana from North Greenland have many similarities to those of Goldfieldia, although in general the front of the glabella is well-

Fig. 71. Trilobites from the Henson Gletscher Formation.

^{1, 3-5, 7, 8.} *Lancastria plana* (Tomashpolskaya, 1960). 1, partial thorax, dorsal view, MGUH 23503 from GGU collection 225707, x 6. 3, damaged complete specimen, dorsal view, MGUH 23500 from GGU collection 315095, x 9. 4, cranidium, partially exfoliated, dorsal view, MGUH 23508 from GGU collection 271485, x 6. 5, hypostome and thorax, dorsal view, MGUH 23502 from GGU collection 301341, x 6.5. 7, partial thorax and pygidium, latex of external mould, MGUH 23504 from GGU collection 315095, x 8.5. 8, damaged cranidium, partially exfoliated, dorsal view, MGUH 23509 from GGU collection 315095, x 9.

^{2, 9.} *Cheiruroides* sp. Å. 2, damaged cranidium, dorsal view, MGUH 23513, x 12. 9, damaged cranidium; dorsal view, MGUH 23512, x 7.5. Both from GGU collection 301338.

^{6.} Ptychoparioid genus and species undetermined A. Damaged cranidium and partial thorax, partially exfoliated, dorsal view, MGUH 23578 from GGU collection 301341, x 2.5.

defined. However, specimens that have an ill-defined glabellar front, with a deep sagittal impression are also known (see Fig. 69.1). Palmer (1964: F8) considered Goldfieldia to be similar to Lancastria in the development of a wire-like anterior rim, but to differ in that an anterior border is defined in Lancastria. Furthermore, Palmer (1964) reported that Lancastria roddyi has no clear indication of S1 being connected to the axial furrow. The material from North Greenland reveals that specimens of Lancastria which lack a clearly defined anterior border are known, and that the S1 glabellar furrows have variable form, and may be isolated from the axial furrow. The similarities of Goldfieldia and Lancastria are such that they are regarded here as synonyms; it is possible that future description of complete specimens of Goldfieldia may prove this synonomy to be incorrect.

Lancastria is also recognised from the Lower Cambrian of China by species referred to *Changaspis*, *Chienaspis* and *Pseudolancastria* (Zhang 1989); Whittington (1995: 555) regarded *Oryctocephalina lancastroides* Shergold, 1969 from Australia as best referred to *Lancastria*.

Chien (1961) attributed *Changaspis*, with type species *C. elongata*, to Lee (MS) but the publication of Lee's work in Egorova *et al.* did not occur until 1963. Subsequent authors have wrongly maintained Lee as the author of *Changaspis*; it should be attributed to Chien (1961). Chien also described *Changaspis micropyge* from the same location. Subsequently, Suvorova (1964: 255) took this species as the type for her monospecific genus *Chienaspis*, considering it to be close to *Lancastria*. Shergold (1969: 53) maintained *Chienaspis* but various Chinese authors have since regarded *Chienaspis* to be invalid, synonymising it with *Changaspis*.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A-11, localities 1, 2 and 6). Age: Early Cambrian, *Olenellus* Zone.

Lancastria? sp. A

Fig. 67.11

Figured material. – Pygidium; MGUH 23499 from GGU collection 218610.

Discussion. – This is known from only a single pygidium. Short (sag.) axis of four rings tapers backwards. There are four pairs of pleural furrows, of which the anterior three are of medium depth and curved strongly posterolaterally. The posterior pair is shallow. Interpleural furrows are faintly impressed. Four pairs of pygidial spines are present. The posterior pair is short, directed posteriorly, remaining pairs are of moderate length and directed strongly backwards. Occurrence in Greenland. – Henson Gletscher Formation, (Figs 8A, 9, locality 5). Age: Early Cambrian, *Olenellus* Zone.

Family Cheiruroididae Suvorova, 1964 Genus *Cheiruroides* Kobayashi, 1935

Type species. – By original designation; *Atops orientalis* Resser & Endo, 1937, from the Middle Cambrian, Redlichia Shales, Misaki, Misakiyama, Manchuria.

Diagnosis. – After Suvorova (1964: 256). Glabella elongate (sag.) with four pairs of indistinct furrows, all pairs joined across sagittal line. Long (exsag.) palpebral lobes. Free cheeks wide (tr.) with short genal spines. Thorax of 14 segments. Small pygidium terminating in a medial spine.

Remarks. – *Cheiruroides* was originally included in the Pagodiidae Kobayashi, 1935. Subsequent authors (Rasetti in Moore 1959; Chernysheva 1960, 1962; Suvorova 1964; Shergold 1969) assigned it to the Oryctocephalidae Beccher, 1897. Zhang (1963, as Chang, and 1980b) expressed his belief that many differences existed between *Cheiruroides* and genuine oryctocephalids, assigning the genus to the Cheiruroididae Chang, 1963.

Cheiruroides sp. A

Fig. 71.2, 9

Figured material. – Cranidium; 23512-23513 from GGU collection 301338.

Other material. - GGU collections 271425, 301336, 301338, 301341, 301351.

Description. - Cranidium with prominent subrectangular glabella, with sides subparallel, or gently convergent forwards, anterior rounded. Axial furrow deep and wide. Three pairs of well-developed glabellar furrows; S1 gently curved and directed obliquely backwards from the axial furrow, of moderate depth and length and occasionally connected across glabella. S2 gently curved, almost transverse, of similar depth to S1 but shorter. S3 short, transverse or directed weakly anteriorly. SO shallows slightly over axial line, curved moderately backwards. Gently convex (tr.) occipital ring with sagittal length about one-tenth that of glabella, weakly developed median node close to posterior margin. Short (sag.) preglabellar field. Narrow (tr.) palpebral areas, transverse width about one-half basal glabellar width. Palpebral lobes gently arcuate, defined by shallow furrows and centred at level of S2. Exsagittal length approximately two-fifths

sagittal glabellar length. Ocular ridges gently curved and defined by shallow furrows. Anterior border furrow deepest distally, shallowing in front of glabella. Defines convex, upturned border of moderate length (sag.). Posterior border short (tr.), narrow (exsag.) adaxially, widening distally. Deep posterior border furrow curved gently anterolaterally. Anterior sections of facial suture convergent in gentle curve forwards. Posterior sections gently convex outwards and moderately divergent.

Sculpture on the glabella is of scattered, low to medium-sized granules with more closely-spaced medium granules on the fixed cheeks.

Discussion. – The anterior margin is more convex, the preglabellar field is wider, and the anterior of the glabella less truncated than in *Cheiruroides dissimilis* Repina in Okunaeva & Repina, 1973.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Oryctocephalid genus and species undetermined A

Fig. 41.1

Figured material. – Partial thorax; MGUH 23514 from GGU collection 313098.

Description. – Thorax formed of at least ten segments with prominent axis tapering backwards. Axial rings with median spine on posterior margin. Pleurae marked by deep, narrow furrows. Long pleural spines directed strongly backwards. Sculpture of coarse ridges on all parts.

Remarks. – The extension of the thoracic pleurae into long posteriorly-directed spines suggests tentative assignment to the Oryctocephalidae.

Occurrence in North Greenland. – Aftenstjernesø Formation, (Fig. 4, locality 4). Age: Early Cambrian, *Olenellus* Zone.

Order Ptychopariida Swinnerton, 1915

Discussion. – The morphologically conservative trilobites referred to in the literature as ptychoparioid are amongst the most abundant forms in the Lower Cambrian faunas of North Greenland. This group of trilobites provides one of the most enigmatic taxonomic problems in Cambrian palaeontology, whether recognised in the restricted sense of Bergström (1973a), or the more general sense of Henningsmoen (in Moore 1959). Indeed, in the opinion of Palmer (in Palmer & Halley 1979: 99) ptychoparioid classification "... provides the greatest problems for suprageneric classification among all the trilobites." This problem is particularly acute in the Lower Cambrian because of the generalised form of many ptychoparioid trilobites. In addition, a general absence of either complete individuals or sufficient disarticulated material, has resulted in a lack of understanding of the intraspecific variation in these trilobites. Attempts at classification, which seem to have created far too many genera, reflect this lack of knowledge.

The approach of workers such as Lochman (1947), Rasetti (1955), Shaw (1962) and more recently Zhang *et al.* (1980) has been to maintain many genus level taxa that are morphologically very similar and which they admit intergrade morphologically. In addition, they allow little variation within taxa. This has led to the formation of many subdivisions at all taxonomic levels. Rasetti (1955: 14) stated that "... if lack of intermediate species were required for generic separation one would have to place most of the Ptychopariidae in a single genus."

Classifications of Lower Cambrian Ptychopariida involve about 20 genera, based on similarities and differences of cranidia (from which the majority are only known), with different workers placing emphasis on different features. As is discussed later, most of these genera cannot be diagnosed and they are therefore considered to be unrecognisable.

The considerable difficulties encountered in ptychoparioid classification were discussed in some detail by Rasetti (1951) who criticised the classification of Lochman (1947) as being too stringent. In particular, Rasetti (1951) highlighted the fact that few of the characters she had used to distinguish ptychoparioid genera (mainly subjective judgements of proportion and convexity) are of any significance and would not even be considered to have any generic importance in other groups of trilobites.

Another factor which has contributed to the present chaos is the possibility of homoeomorphy of cranidia amongst the ptychoparioid trilobites, as emphasised by Palmer (1958). That homoeomorphy exists amongst Cambrian genera has been demonstrated in the Dolichometopidae by Rasetti (1951), with further examples being known in the Corynexochidae (Palmer, 1958). Palmer (1968) also recognised apparently unpredictable variability in many Lower Cambrian ptychoparioid samples.

The problems of identifying recognisable genera amongst the early ptychoparioids necessarily cause complications for suprageneric classification. In agreement with Palmer (in Palmer & Halley 1979) it is accepted that in general suprageneric groupings cannot be recognised with any certainty. Palmer did suggest that at least one suprageneric grouping might be recognised which he termed the 'kochaspid trilobites', an informally-defined group discussed below.

Blaker (1986) proposed that the distribution of these

generalised taxa in time and space that will be of critical importance in determining which genera will be placed into these higher level groupings but this is no longer advocated. As will be evident from the ensuing discussions, there is at present no immediate solution to ptychoparioid classification, and there is a real need for more information based on the complete trilobite exoskeleton if these taxonomic problems are to be solved. Indeed, in a discussion of ptychoparioid classification, Palmer (1968: B74) used the phrase "... systematic quagmire" to describe the complexities of this group. As a consequence of these difficulties the taxonomy employed here is deliberately conservative.

The material from North Greenland offers the possibility to study the range of at least cranidial variation within what is considered to be a single ptychoparioid species, since large numbers of specimens of all sizes are available from individual collection localities.

Family Ptychopariidae Matthew, 1887 Genus *Ptychoparella* Poulsen, 1927

Synonyms. – Syspacephalus Resser, 1936, Elrathina Resser, 1937 Eoptychoparia Rasetti, 1955.

Type species. – By original designation (Poulsen 1927: 279). *Ptychoparella brevicauda* Poulsen, 1927 from the Cape Wood Formation of Inglefield Land, North-West Greenland (see also Poulsen 1964: 39).

Diagnosis. – Diagnosis of *Elrathina* after Palmer (in Palmer & Halley 1979: 103). Anteriorly convergent anterior sections of facial sutures; glabella strongly rounded across front with subparallel or very slightly convergent sides; small palpebral lobes situated slightly anterior to glabellar midlength; free cheeks lack significant development of genal spines. Thorax of 15-19 segments and a simple nonspinose pygidium.

Remarks. – This species described below has been identified in several samples, with one particularly large collection (GGU 301346 from the Henson Gletscher Formation, Figs 8A, 10, locality 1) giving an insight into the extreme range of cranidial morphology that may be encountered within a population. Cranidial morphology ranges from an *Antagmus*-type end member through to an *Elrathina*-type and, if found in isolation, the end members of this apparent continuum would probably be regarded as being members of different genera. No breaks have been detected in the spectrum of morphology.

The diagnosis and following description are based on specimens that are of *Elrathina* aspect, for complete specimens of this type are known, and they are also dominant within the sample. However, *Elrathina* is considered to be a junior synonym of *Ptychoparella* Poulsen, 1927. Babcock (1994a: 110) considered *Elrathina* to be a

junior synonym of *Syspacephalus* Resser, 1936 and this genus too is here placed in synonymy with *Ptychoparella*.

Ptychoparella is one of several generalised taxa of early ptychoparioids described from the Middle Cambrian of Inglefield Land, North-West Greenland (Poulsen 1927, 1964). Outside the Great Basin of the western United States, Elrathina is generally considered to be a diagnostic element of Middle Cambrian Bathyuriscus -Elrathina faunas. Elrathina antiqua Palmer in Palmer & Halley 1979 was previously the oldest known representative of the genus, occurring in the Middle Cambrian (Albertella Zone) of the southern Great Basin. Within Greenland, Elrathina has been reported by Palmer & Peel (1979) from the Middle Cambrian Ekspeditions Bræ Formation (Fig. 2). As a junior synonym of Syspacephalus, it was described from the Middle Cambrian beds of the Henson Gletscher Formation of northern Nyeboe Land by Babcock (1994a).

Ptychoparella sp. A

Figs 72.1, 3, 4; 73-76; 77.1-4, 7, 8; 78; 79

1986 *Ptychoparella brevicauda* Poulsen, 1927; Blaker p. 70.

Figured material. - Anaprotaspid; MGUH 23554-23555 from GGU collection 225714A. Complete specimen; MGUH 23515 from GGU collection 301344. Cranidium and thorax; MGUH 23516 from GGU collection 298553. Cranidium and partial thorax; MGUH 23517-23519 from GGU 298553, MGUH 23520 from GGU collection 301344. Cranidium; MGUH 23521-23535 from GGU collection 301346, MGUH 23536-23538 from GGU collection 298553, MGUH 23541-23550 from GGU collection 225709, MGUH 23551-23553 from GGU collection 225714, MGUH 23556-23567 from GGU collection 225714A. Free cheek; MGUH 23539-23540 from GGU collection 298553, MGUH 23570, 23574-23575 from GGU collection 225714A. Pygidium; MGUH 23568-23569, 23572-23573, 23576-23577, 24386-24387 from GGU collection 225714A. Thoracic segment; MGUH 23571 from GGU collection 225714A.

Other material. – GGU collections 218584, 218681, 225707, 225709 (abundant), 225714, 271750, 271756, 298547, 298553, 301340 (abundant), 301344, 301346 (abundant), 315107 (abundant) and 315112.

Description. – Cranidium gently to moderately convex (tr. & sag.), with strongly convex glabella (tr.) that in lateral profile is almost horizontal over posterior two-thirds, sloping down anteriorly to preglabellar field. Sagittal length of glabella approximately three-quarters that of cranidium. Glabellar sides subparallel or tapering gently



Fig. 73. *Ptychoparella* sp. A. Henson Gletscher Formation. 1, cranidium, partially exfoliated, dorsal view, MGUH 23541, x 17. 2, cranidium, partially exfoliated, dorsal view, MGUH 23542, x 14. 3, cranidium, partially exfoliated, dorsal view, MGUH 23543, x 8. 4, cranidium, internal mould, dorsal view, MGUH 23544, x 10. 5a, b, cranidium, partially exfoliated, dorsal and lateral views, MGUH 23545, x 7. 6a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23545, x 7. 6a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23545, x 7. 6a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23545, x 7. 6a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23545, x 7. 6a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23545, x 7. 6a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23545, x 7. 6a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23545, x 7. 6a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23545, x 7. 6a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23545, x 7. 6a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23545, x 7. 6a, b, cranidium, internal mould, dorsal view, MGUH 23547, x 9. 8, cranidium, partially exfoliated, dorsal view, MGUH 23552 from GGU collection 225714, x 11. 9, cranidium, partially exfoliated, dorsal view, MGUH 23547, x 8. From GGU collection 225709 unless stated.



Fig. 74. *Ptychoparella* sp. A. Henson Gletscher Formation. 1, anaprotaspid, dorsal view, MGUH 23554, x 54. 2, anaprotaspid, dorsal view, MGUH 23555, x 55. 3, early meraspid cranidium, dorsal view, MGUH 23556, x 53. 4, early meraspid cranidium, dorsal view, MGUH 23557, x 55. 5, early meraspid cranidium, dorsal view, MGUH 23558, x 55. 6, early meraspid cranidium, dorsal view, MGUH 23559, x 53. 7, early meraspid cranidium, dorsal view, MGUH 23560, x 53. 8, early meraspid cranidium, dorsal view, MGUH 23561, x 53. 9, middle meraspid cranidium, dorsal view, MGUH 23562, x 26. 10, middle meraspid cranidium, dorsal view, MGUH 23564, x 26. 11, middle meraspid cranidium, dorsal view, MGUH 23564, x 26. 12, late meraspid/holaspid cranidium, dorsal view, MGUH 23565, x 26. 13, late meraspid/holaspid cranidium, dorsal view, MGUH 23566, x 26. All from GGU collection 225714A.

forwards to rounded anterior, laterally defined by broad (tr.) furrows of medium depth that are continuous with narrower preglabellar furrow. Three pairs of glabellar furrows; S1 of variable depth, directed strongly backwards from the axial furrow, S2 directed less steeply backwards, reaches to axial furrow where depth increases slightly. S3 very diffuse and poorly-impressed. Occipital furrow straight, shallowest axially, often deflected forwards over axial line. Occipital ring simple, gently convex transversely, in lateral profile slightly upturned, with centrally positioned axial node. Glabella separated from anterior border by gently downsloping preglabellar field; sagittal length about one-fifth that of glabella. Anterior border defined by narrow furrow that shallows slightly axially. Border convex and arched in anterior view, occasionally with slight median swelling. Palpebral areas and posterior areas of fixed cheek gently convex; transverse width of palpebral areas variable between one-half and two-thirds basal glabellar width. Palpebral lobes defined by narrow, diffuse furrow; exsagittal length approximately one-quarter sagittal glabellar length. Lobes straight and directed weakly posterolaterally, centred at about two-thirds glabellar length. Ocular ridges gently curved and poorly defined. Posterior border directed slightly posterolaterally, very narrow adaxially, gradual increase in width to point of geniculation, then expanding (exsag.) more rapidly to rounded terminations. Posterior border furrow wide (exsag.) and shallow axially, increasing in both width and depth distally. Anterior sections of facial suture very slightly curved forward from palpebral lobe, with overall convergence. Posterior sections moderately divergent in gentle curve.

Free cheek with wide, gently convex (tr.) ocular platform. Well defined, convex lateral border defined anteriorly by narrow furrow, posteriorly by alteration in exoskeletal slope. Lateral margin gently curved, continuous with genal spine of unknown proportions.

Thorax formed of 17 segments, gradual increase in width over the anterior six, then tapering posteriorly. Axis decreases in width (tr.) from anterior segment; rings



Fig. 75. *Ptychoparella* sp. A. Henson Gletscher Formation. 1, late meraspid/holaspid cranidium, dorsal view, MGUH 23567, x 26. 2, transitory pygidium, dorsal view, MGUH 23568, x 53. 3, transitory pygidium, dorsal view, MGUH 23569, x 53. 4, free cheek, dorsal view, MGUH 23570, x 105. 5, partial thoracic segment, posterior view, MGUH 23571, x 26. 6, transitory pygidium, dorsal view, MGUH 23572, x 54. 7, transitory pygidium, dorsal view, MGUH 23573, x 53. 8, free cheek, dorsal view, MGUH 23574, x 26. 9, free cheek, ventral view, MGUH 23575, x 26. 10, late meraspid/holaspid pygidium, MGUH 23576, x 53. 11, late meraspid/holaspid pygidium, MGUH 23577, x 53. 12, late meraspid/holaspid pygidium, MGUH 24386, x 54. 13, late meraspid/holaspid pygidium, MGUH 24387, x 53. All from GGU collection 225714A.

of moderate convexity (tr.), defined by narrow inter-ring furrows of moderate depth. Transverse width of axial rings approximately one-quarter that of segment. Wellimpressed pleural furrows widest (exsag.) at point of geniculation, distally narrowing and increasing in depth, reaching almost to pleural extremities which are bluntly rounded without a spine.

Pygidium subellipitical in outline, sagittal length onethird maximum transverse width. Axis tapers gently backwards, not reaching posterior margin. Weak indications of three axial rings; anterior width of axis approximately two-fifths maximum transverse pygidial width. Pleural fields with at least three pairs of pleural furrows that do not reach to pygidial margin. No border evident.

Sculpture of the cranidium consists of closely-spaced, low granules on the occipital ring and posterior glabella, with a similar arrangement on the anterior border. Extremely low granules occur on all other parts of the cranidium. Medium granules form the sculpture of the thorax, being particularly concentrated on the distal parts of the

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posterior pleural bands and more widely scattered on all other parts. Widely distributed, medium granules on the pygidial pleural fields.

Discussion. – There is considerable variation in morphology within the populations of this species and in particular of four main cephalic features; glabellar outline, strength of impression of glabellar furrows, relief of ocular ridges and amount of medial expansion of the anterior border. The degree of impression of glabellar furrows and relief of the ocular ridges is markedly different on internal and external moulds, specimens that are exfoliated showing enhancement of both features (see Fig. 79.6, for example). This enhancement, a feature common to all trilobites, has been used as a generic character by some previous workers (e.g. Rasetti 1951).

The largest available population (from GGU collection 301346) displays the widest range of cranidial morphology (cf. Figs 73, 77, 79). It is tempting to suggest that as one extreme of this wide range of morphology resembles



Fig. 76. *Ptychoparella* sp. A. Henson Gletscher Formation. 1a, b, cranidium, internal mould, dorsal and lateral views. MGUH 23531 from GGU collection 301346, x 5. 2, complete specimen, latex of external mould, MGUH 23515 from GGU collection 301344, x 4. 3a, b, cranidium, internal mould, dorsal and lateral views, MGUH 23527 from GGU collection 301346, x 6.5. 4, free cheek, internal mould, dorsal view, MGUH 23539 from GGU collection 298553, x 9.

Elrathina and the other resembles *Antagmus* Resser, 1936 that these two genera are synonyms. The range of variation displayed could also accommodate species referred to several other genera (e.g. *Onchocephalus* Resser, 1937 and *Piaziella* Lochman, 1947). The possibility therefore exists that many species belonging to several genera in different families, as presently recognised, could in fact be representatives of a single, highly variable species. Many of these forms, as previously remarked, are based on cranidia alone, making such a sweeping large scale synonomy unwise. One example, however, is discussed below.

Previously Blaker (1986), based on examination of only small populations, described the Antagmus-type end member as being Ptychoparella brevicauda Poulsen, 1927. Following Poulsen (1927), Resser (1937, 1938) and Lochman (1947) assigned Lower Cambrian American material to several new species of Ptychoparella. Rasetti (1955: 7), however, considered that no Lower Cambrian species should be referred to that genus which he confined to the Middle Cambrian type species. He established a new genus Eoptychoparia to incorporate the Lower Cambrian species. Shaw (1962) and Poulsen (1964) both agreed that the use of *Ptychoparella* should be restricted to the type species until the genus was better known. Study of the Henson Gletscher material confirms that specimens referable to Poulsen's (1927, 1964) concept of Ptychoparella occur in the Lower Cambrian. Rasetti (1955: 13) remarked that the species he attributed to Eoptychoparia "... are about average" for Lower Cambrian ptychoparioids, and that the genus was difficult to characterise since it intergraded with Antagmus, Piaziella and Onchocephalus. Rasetti also considered that Eoptychoparia essentially corresponded to the concept of Ptychoparella employed by Resser (1937, 1938) and Lochman (1947), not to Poulsen's type species. Palmer (in Palmer & Halley 1979) regarded Eoptychoparia to be perhaps the "most central" of the generalised Early and Middle Cambrian ptychoparioids, distinguishing it from Piaziella on its narrower (tr.) fixed cheeks and a lack of distinct median inbend to the anterior border. This contradicts Shaw (1962: 343) who, together with other characters, used the presence of a median inbend to separate Eoptychoparia from Ptychoparella.

The concepts of *Ptychoparella* and *Eoptychoparia* are therefore unreliable and unsatisfactory. Rasetti's (1955) concept that only Middle Cambrian forms may be referred to *Ptychoparella* and Lower Cambrian forms to *Eoptychoparia* is not tenable, for it is not based on morphology; in any case Rasetti (1963: 582) subsequently recognised Middle Cambrian species of *Eoptychoparia*.

Following study of the type material of both type species, *Eoptychoparia* is considered to be congeneric with *Ptychoparella* and both are considered to be synonymous with *Elrathina*. As first described form, *Ptychoparella* has seniority.



Fig. 77. Trilobites from the Henson Gletscher Formation.

1-4, 7, 8. *Ptychoparella* sp. A. 1, cranidium and thorax, dorsal view, MGUH 23517 from GGU collection 298553, x 5. 2, cranidium and damaged thorax, dorsal view, MGUH 23518 from GGU collection 298553, x 5. 3, damaged cranidium and thorax, dorsal view, MGUH 23516 from GGU collection 298553, x 4.5. 4a, b, cranidium, partially exfoliated, dorsal and lateral views, MGUH 23538 from GGU collection 298553, x 5.5. 7, free cheek, partially exfoliated, dorsal view, MGUH 23540 from GGU collection 298553, x 5. 8, cranidium and partial thorax, latex of external mould, dorsal view, MGUH 23519 from GGU collection 298553, x 5. 5, 6. *Zacanthopsis contracta* Palmer, 1964. 5, cranidium, internal mould, dorsal view, MGUH 23462 from GGU collection 301343, x 10.5. 6, cranidium, partially exfoliated, dorsal view, MGUH 23458 from GGU collection 298544, x 5.5.

Ontogeny. – Palmer (1958) in a study of silicified material of the Early Cambrian *Crassifimbra walcotti* (Resser, 1937) recognised five developmental stages in the growth series and the present material of *Ptychoparella* sp. A has been compared to these stages. Palmer (1958: 165) defined 5 stages: 1, anaprotaspid; 2, metaprotaspid; 3, early meraspid; 4, middle meraspid; 5, late meraspid and holaspid.

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Stage 1: anaprotaspid (Fig. 74.1-2). Exoskeleton subquadrate in outline with a pair of widely-spaced spines along the posterior margin. In dorsal view the glabella is very narrow (tr.) over the posterior three-quarters, expanding rapidly anteriorly and merging with the marginal border. Glabella defined laterally by shallow furrows. Weakly developed segmental division of glabella, but not of cheeks. 'Occipital ring' discernible.

Stage 2: metaprotaspid. The metaprotaspid stage of growth has not been recognised in the material from North Greenland.

Stage 3: early meraspid (Fig. 74.3-8). Cranidium subtrapezial in outline with maximum transverse width across posterior border. Narrow (tr.) glabella expands anterior to the occipital ring and reaches to the cranidial margin. Glabella defined by narrow, shallow furrows. Occipital and three other furrows continuous across glabella. Posterior border and furrow present. Anterolateral corners of glabella merge with ocular ridge; palpebral lobe poorly differentiated. Low granules on distal parts of fixed cheeks, occasionally on entire cranidium.

Stage 4: middle meraspid (Fig. 74.9-11). Cranidium subtrapezial in outline being broadest at the level of the occipital furrow. Glabella parallel-sided in front of occipital ring, then expanded anteriorly and reaching to inner margin of narrow (sag.) border. Ocular ridge weakly evident, and palpebral lobe evident but indistinctly differentiated from it. Occipital ring clearly delimited, and weak indications of at least two other transglabellar furrows. Fixed cheeks with sculpture of closely-spaced medium granules, low granules on posterior of glabella.

Stage 5: late meraspid and holaspid (Figs 74.12-13 and 75.1). These two stages of growth are indistinguishable. Palmer (1958) considered that the onset of maturity was indicated by the development of a preglabellar field and more parallel-sided glabella in late meraspides, with holaspides having a glabella that tapers forward. Late meraspides retain a somewhat subdued granular sculpture, which has not been observed on specimens assigned to the holaspid stage.

Remarks. – The stages of growth recognised by Palmer (1958) for specimens in the meraspid and holaspid periods are based on changes in morphology during the development of the cranidium. No complete specimens have been recovered among the phosphatic material of *Ptychoparella* sp. A and specimens of other exoskeletal parts are not readily assignable to a particular stage. Transitory pygidia are subrectangular in outline with a marked median indentation along the posterior margin which is much more pronounced in smaller specimens. The axis tapers backwards and reaches almost to the posterior margin. Sculpture is of coarse granules on the pleural fields and low granules on the axis. Transitory pygidia (Fig. 75) of the presumed late meraspid stage are sub-



Fig. 78. *Ptychoparella* sp. A. Henson Gletscher Formation. 1, damaged cranidium, dorsal view, MGUH 23521 from GGU collection 301346, x 5. 2, cranidium, internal mould, dorsal view, MGUH 23532 from GGU collection 301346, x 7. 3, cranidium, partially exfoliated, dorsal view, MGUH 23523 from GGU collection 301346, x 7 (see also Fig 79.5). 4, cranidium, partially exfoliated, dorsal view, MGUH 23534 from GGU collection 301346, x 7. 5, cranidium, internal mould, dorsal view, MGUH 23535 from GGU collection 301346, x 7. 8, cranidium, partially exfoliated, dorsal view, MGUH 23528 from GGU collection 301346, x 9.



Fig. 79. *Ptychoparella* sp. A. Henson Gletscher Formation. 1a, b, cranidium, partially exfoliated, dorsal and lateral views, MGUH 23537 from GGU collection 298553, x 5.5. 2, cranidium, partially exfoliated, dorsal view, MGUH 23533, x 5. 3, damaged cranidium, internal mould, dorsal view, MGUH 23524, x 7. 4, cranidium, partially exfoliated, dorsal view, MGUH 23522, x 5.5. 5, cranidium, partially exfoliated, lateral vire, MGUH 23523, x 7 (see also Fig. 78.3). 6, cranidium, partially exfoliated, dorsal view, MGUH 23523, x 6. 8, cranidium, partially exfoliated, dorsal view, MGUH 23526, x 7.5. 9, cranidium, internal mould, dorsal view, MGUH 23525, x 13. 10, cranidium, internal mould, dorsal view, MGUH 23529, x 8.5. 11, damaged cranidium and partial thorax, dorsal view, MGUH 23520 from GGU collection 301344, x 7. From GGU collection 301346 unless stated.

ovate in outline. Isolated free cheeks (Fig. 75) which have not been assigned to growth stages, are simple with short genal spines, have no distinct separation of the border from the genal platform and are without sculpture.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, 11, localities 1 and 6). Age: Early Cambrian, *Olenellus* Zone.

Ptychoparioid genus and species undetermined A

Fig. 71.6

Figured material. – Fragmentary cranidium and partial thorax; MGUH 23578 from GGU collection 301341.

Description. - Glabella moderately convex (tr. & sag.), lateral margins concave, overall convergence forwards from SO; anterior margin gently curved. Axial furrow narrow (tr.), slight anterior shallowing, continuous with preglabellar furrow. S1 directed strongly backwards, not reaching across axial line; S2 shorter, shallower and angled less steeply backwards. S3 poorly-impressed, transverse and isolated from axial furrow. Occipital furrow wide (exsag.), shallowing adaxally. Occipital ring simple with median node close to posterior margin. Frontal area slopes gently downwards with long (sag.) preglabellar field. Anterior border furrow approximately transverse, defining gently convex border of moderate length (sag.). Palpebral lobes short (exsag.), straight, defined by shallow furrow. Exsagittal length about one-quarter sagittal glabellar length. Ocular ridges wide (exsag.), straight and divided by shallow median groove. Wide (tr.) posterior area of fixed cheek. Posterior border furrow very wide (exsag.), deepest distally. Posterior border narrow and transverse from axial furrow to geniculation, then directed posterolaterally, increasing in width distally. Anterior sections of facial suture initially directed exsagittally from palpebral lobe, then turned strongly axially. Posterior sections directed backwards at an angle of approximately 50 degrees to an exsagittal line until level with midpoint of L1, then directed sharply posteriorly.

Thorax formed of at least seventeen segments of about equal width over the anterior twelve, tapered gently backwards over the posterior five. Pleurae very wide (tr.), axial rings gently convex (tr.). Narrow axial furrow of moderate depth. Pleurae with broad furrow, very gently sigmoidal in outline and deepest distally, shallowest over midlength. Pleurae extend into short, posteriorly directed, slender spines.

Sculpture of low granules of moderate spacing on gla-

bella and thoracic axis, very low granules on all other parts.

Discussion. - The double eye ridge of this specimen is relatively uncommon amongst the ptychoparioids, and has not previously been recorded in any other Lower Cambrian form. Such eye ridges, however, are known from two Middle Cambrian genera; Prohedinia Lermontova & Chernysheva in Chernysheva 1950 and Chancia Walcott, 1924. This specimen from North Greenland differs from Prohedinia (type species Prohedina attenuata Lermontova & Chernysheva in Chernysheva 1950 from Siberia) in terms of its gently convex border that is not distinctly upturned or markedly narrower than the preglabellar field. The sculpture of the anterior border is more reminiscent of *Chancia* (type species *Chancia ebdome* Walcott, 1924 from the Spence Shale, Idaho, U.S.A). However, the present form differs in that the sagittal length of the frontal area is not greater than half of the sagittal glabellar length (exclusive of the occipital ring), a feature by which Chancia was diagnosed (see Palmer in Palmer & Halley 1979: 103). The Greenland specimen also differs from Chancia in that the palpebral lobes are situated more anteriorly and the glabellar sides are moderately concave.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 10, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Ptychoparioid genus and species undetermined B

Fig. 51. 6, 9, 11

Figured material. – Cranidium; MGUH 23579-23580 from GGU collection 270563, MGUH 23581 from GGU collection 270568.

Discussion. – This form is represented by three cranidia and is characterised by a bluntly rounded, anteriorly-tapering glabella with deep axial furrows. The anterior border is narrow with variable medial expansion; the occipital ring is simple and the short (exsag.) palpebral lobes are centred at approximately the glabellar mid-length. Three pairs of glabellar furrows are weakly defined, though the depth of impression may be related to preservation.

This rather generalised ptychoparioid is similar in form to specimens assigned to *Ptychoparella* sp. A, but preservation in coarse sandstone has obscured much detail.

Occurrence in North Greenland. – Sæterdal Formation, (Fig. 8B). Age: Early Cambrian, *Olenellus* Zone.

Ptychoparioid genus and species undetermined C

Fig. 51.7

Figured material. – Cranidium; MGUH 23582 from GGU collection 270563.

Other material. - GGU collection 270563.

Discussion. – Two simple ptychoparioid cranidia are characterised by a prominent, wide (sag.) anterior border with slight medial expansion, anterior sections of the facial suture that are initially divergent, and then turn strongly axially over the border. Gently curved ocular ridges are pronounced and palpebral lobes are centred slightly posteriorly of the glabellar midlength. Narrow (tr.) glabella tapers moderately forward, is rounded anteriorly, and has three pairs of poorly-impressed glabellar furrows.

The specimens were found in association with ptychoparioid genus and species undetermined B from which they are distinguished primarily on the morphology of the anterior border. These cranidia also have some similarities to specimens assigned to *Ptychoparella* sp. A and provide a good example of the difficulties of classification within this group. Taken in isolation, the material from the Sæterdal Formation appears to represent two species. When compared to the much larger population of *Ptychoparella* sp. A from the Henson Gletscher Formation in Freuchen Land, a strong case exists for regarding all of the specimens as conspecific. A conservative approach has been taken on account of the small amount of material available from the Sæterdal Formation and its preservation in coarse sandstone.

Occurrence in North Greenland. – Sæterdal Formation, (Fig. 8B). Age: Early Cambrian, *Olenellus* Zone.

Systematic position uncertain Genus *Perissopyge* Blaker, Nelson & Peel, 1997

Type species. – *Perissopyge phenax* Blaker, Nelson & Peel, 1997 from the Lower Cambrian Henson Gletscher Formation of central North Greenland (Figs 8A, 11, locality 6).

Diagnosis. – After Blaker *et al.* (1997). Glabella with slightly concave sides. Preglabellar field present. Palpebral areas very wide (tr.); long, gently curved ocular ridges and short (exsag.) palpebral lobes. Hypostome fused to rostral plate; anterior lobe of middle body with median swelling. Thorax of seven segments. Large, triangulate

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pygdium with long (sag.) axis of up to 14 rings. Pleural regions crossed by up to 10 pairs of pleural furrows. Very narrow border. Granular sculpture on all exoskeletal parts except hypostome.

Discussion. – *Perissopyge* was described by Blaker *et al.* (1997) on the basis of two species, the type species *P. phenax* from the Henson Gletscher Formation (*Olenellus* Zone) of central North Greenland, and *P. triangulata* from the Lower Cambrian Harkless Formation of Nevada.

Blaker *et al.* (1997) noted that the cranidium of *Perissopyge* is similar to that of *Aldonaia* Lermontova, 1940 but that there are considerable differences in the form of the thorax and pygidium. It was concluded that *Perissopyge* is not closely related to *Aldonaia* and that it could not be included within the Aldonaiidae or any known family. Even the supra-generic classification of *Perissopyge* presents difficulties. The presence of a preglabellar field of the type seen in *Perissopyge* is typical of ptychoparioids where the hypostome is generally separated from the rostrum by a definite gap, so that the hypostome was free. *Perissopyge* has developed a preglabellar field but the hypostome remains in contact with the rostrum, a form of hypostomal development typical of corynexochids.

Perissopyge phenax Blaker, Nelson & Peel, 1997

Fig. 80

1997 Perissopyge phenax Blaker, Nelson & Peel, pl. 1, 2

Holotype. – Pygidium; MGUH 23584 from GGU collection 271756, figured by Blaker *et al.* (1997, pl. 2, fig. 1a, b).

Figured paratypes. – Cranidium; MGUH 23585-23586 from GGU 271756, MGUH 23587 and 23589 from GGU collection 225703. Free cheek; MGUH 23590 from GGU collection 271756. Hypostome; MGUH 23591 from GGU collection 225703. Pygidium; MGUH 23592 from GGU collection 271756, MGUH 23594 from GGU collection 225703.

Other material. – GGU collections 225702-225704, 271756 (abundant).

Discussion. – Complete specimens of *P. phenax*, the type species of *Perissopyge*, are not known. In *P. triangulata*, from the Lower Cambrian Harkless Formation of Miller Mountain, Nevada, there are seven segments in the thorax which is of about constant width over the anterior five, tapering gently over the posterior two. The thoracic axis is narrow (tr.) and tapers backwards from the anteri-



Fig. 80. *Perissopyge phenax* Blaker, Nelson & Peel, 1997. Henson Gletscher Formation. 1, paratype, damaged cranidium, partially exfoliated, dorsal view, MGUH 23585 from GGU collection 271756, x 4. 2, cranidium, paratype, internal mould, dorsal view, MGUH 23589 from GGU collection 225703, x 4. 3, free cheek, paratype, dorsal view, MGUH 23590 from GGU collection 271756, x 3. 4, cranidium, paratype, latex of external mould, dorsal view, MGUH 23587 from GGU collection 225703, x 4. 5a, b, cranidium, paratype, partially exfoliated, dorsal and lateral views, MGUH 23586 from GGU collection 225703, x 4. 5a, b, cranidium, paratype, partially exfoliated, dorsal and lateral views, MGUH 23586 from GGU collection 225703, x 4. 5a, b, cranidium, paratype, partially exfoliated, dorsal and lateral views, MGUH 23594 from GGU collection 225703, x 3. 7a, b, pygidium, paratype, internal mould, lateral and dorsal views, MGUH 23592 from GGU collection 271756, x 7. 8, hypostome and rostral plate, paratype, ventral view, MGUH 23591 from GGU collection 225703, x 7.

or ring. Pleurae are wide (tr.), and terminate in short, posterolaterally directed spines; furrows are wide (exsag.), of moderate depth and extend to the pleural spine bases.

In addition to its Greenland occurrence, *Perissopyge phenax* is also identified from an undescribed section of the Lower Cambrian Sekwi Formation in the Yukon Territory, Canada (GSC locality 99785, section FN 83-5, Selwyn Basin). Dr W. H. Fritz (Geological Survey of Canada) kindly brought these specimens to our attention.

Occurrence in North Greenland. – Henson Gletscher Formation, (Figs 8A, 11, locality 6). Age: Early Cambrian, *Olenellus* Zone.

Genus Labradoria Resser, 1936

Synonym. - Sinolenus Kobayashi, 1944.

Type species. – By original designation; *Conocephalites misera* Billings, 1861 from Lower Cambrian strata of Labrador, Canada.

Remarks. – Ivshin (1957) added *Labradoria* to the Edelsteinaspidae Hupé, 1953; this assignment was challenged by Kobayashi (1961) who considered it to be more like a protolenid. However, as *Labradoria* is known from only small populations of cranidia and free cheeks, its taxonomic position is difficult to assess. Henningsmoen (in Moore 1959) assigned *Labradoria* to Family Uncertain, while Fritz (1973) proposed that *Labradoria* is probably a ptychoparioid. In the absence of the other exoskeletal elements no assignment at the family level is made here.

Henningsmoen (in Moore 1959) also assigned Sinolenus to Family Uncertain, and distinguished it from Labradoria on the basis of shorter (exsag.) palpebral lobes. The palpebral lobes are also short (exsag.), however, in the holotype cranidium of the type species Labradoria misera (Billings, 1861) as illustrated by Resser (1937, pl. 8, figs 23, 24); they do not reach to the posterior border furrow, as was described by Henningsmoen (in Moore 1959). That Labradoria has short palpebral lobes is also confirmed by illustrations of L. hespera in Fritz (1973). The line drawing of Labradoria in Henningsmoen (in Moore 1959) is very misleading since the morphology of the ocular ridges and palpebral lobes is incorrect, as is the continuation of S3 across the axial line. There are no differences in palpebral lobe morphology between the two genera. Thus, Sinolenus is synonymised with Labradoria.

Emended diagnosis. – Wide (tr.) glabella reaches to anterior border furrow. Three pairs of glabellar furrows, all directed backwards and S1 always joined across

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axial line, S2 occasionally joined. Short (sag.) occipital ring with spine on posterior margin. SO continuous and posteriorly concave. Granular sculpture on cranidium.

Labradoria misera? (Billings, 1861)

Fig. 20.6

- 1861 Conocephalites misera Billings, p. 11, fig. 14.
- 1937 Labradoria elongata Resser, p. 48, figs 28-30 (after Fritz 1973)
- 1937 Labradoria misera (Billings); Resser, p. 47, pl. 8, figs 23-27. (Includes complete synonomy)
- 1979 Labradoria, Palmer in Hurst & Peel, p. 43

Type material. – Resser (1937) designated a cranidium (National Museum of Canada 430b) from the Lower Cambrian at Forteau, L'Anse au Loup, Labrador, Canada, to be the type of the species.

Figured material. – Cranidium; MGUH 23595 from GGU collection 270505.

Description. - Cranidium subquadrate in outline. Prominent glabella highly convex (tr.). Glabella tapers anteriorly, sides gently convex between SO and S3, slight contraction at level of S3, anterior broadly rounded and reaching to anterior border furrow. Three well-impressed pairs of glabellar furrows, all reaching to axial furrow. S1 of moderate length and depth, directed backwards at angle of about 55 degrees to an exsagittal line, and connected across glabella by furrow of reduced depth and width that is curved posteriorly. S2 directed backwards at similar angle to S1, of slightly reduced length and depth, not connected across glabella. S3 of similar depth to S2, shorter and very gently arcuate. SO deep, narrow furrow that is continuous and moderately concave posteriorly. Occipital ring short (sag.), gently convex (tr.), sagittal length approximately one-tenth that of glabella. Axial furrow posteriorly narrow and of moderate depth, with depth and width gradually increasing until level of S3, shallowing anteriorly. Transverse width of palpebral areas slightly less than one-half that of glabella at base. Palpebral lobes arcuate, centred at level of S2, exsagittal length about one-third sagittal glabellar length. Palpebral lobes defined by shallow, broad furrow. Ocular ridges short, straight and defined posteriorly by narrow furrow, anteriorly by change in exoskeletal slope. Preocular cheek slopes moderately anterolaterally. Anterior border furrow deepens in front of glabella, and is deflected slightly forwards, abaxially of moderate depth and width. Anterior border gently convex and strongly upturned. Sagittal length of border approximately one-ninth that of glabella. Posterior border furrow narrow axially, widening rapidly distally. Posterior border directed very slightly posterolaterally, subtriangulate in outline. Anterior sections of facial suture with overall divergence, initially suture gently convex forward from palpebral lobe to border, then turned adaxially over the border. Posterior sections unknown.

Sculpture consists of coarse, closely-spaced granules on the glabella, with similar but more widely-spaced granules on the fixed cheeks. Anterior border with densely-spaced, medium size granules.

Discussion. – The single cranidium is most like *Labradoria misera* (Billings, 1861) from the Lower Cambrian of Labrador. This species is not well described or figured, and the only photographic illustrations appear to be by Resser (1937). Differences from the single specimen from the Kap Troedsson Formation are that the glabella is proportionately wider (tr.), S2 is joined across the glabella by a very shallow furrow, and there is a median node on the posterior margin of the occipital ring. As the type material consists of only three cranidia the variability of cranidial morphology can not be ascertained, and the single cranidium from Wulff Land is tentatively assigned to *Labradoria misera*.

The specimen from North Greenland occupies somewhat of an intermediate position between L. misera and Labradoria hespera Fritz, 1973 for it shares with L. hespera the high convexity of the glabella and wider (tr.) palpebral areas, both of which are features used by Fritz (1973) to distinguish L. hespera from L. misera. Additionally, Fritz (1973: 17) separated L. hespera on S2 not being connected across the glabella but illustrations (Fritz 1973, pl. 4, figs 21, 24) show that S2 is connected across the axial line by a narrow furrow that is gently concave posteriorly. L. hespera is based on a sample of only eight cranidia and two free cheeks. Within this small population there is considerable variation in glabellar furrow configuration which is the main morphological feature used by Fritz (1973) to distinguish this species. Study of variation in a larger population, with a more complete range of morphology, would probably result in unification of L. misera, L. hespera and the single cranidium described here from North Greenland in a single species.

Palmer in Hurst & Peel (1979) reported *Labradoria* from a thin limestone coquina occurring in the transition from the Buen Formation to overlying Cambrian dolomites in southern Wulff Land. This is the specimen described here and it is now known to be derived from the Kap Troedsson Formation.

Occurrence in North Greenland. – Kap Troedsson Formation, (Fig. 6, locality 1). Age: Early Cambrian, *Olenellus* Zone.

Genus Alacephalus Repina, 1960

Type species. – *Alacephalus contortus* Repina, 1960, from the Lower Cambrian of Tuva, western Sayan, Russia.

Alacephalus? davisi Lane & Rushton, 1992

Fig. 81

1992 Alacephalus? davisi Lane & Rushton, p. 8, pl. 1

Figured material. – Damaged complete specimen, MGUH 21143 from GGU collection 319544.

Discussion. – The only known specimen of this unusual trilobite was described by Lane & Rushton (1992) from the uppermost Buen Formation of northern Freuchen Land where it is associated with sponges described by Rigby (1986). Subsequent collecting from the locality in 1994 yielded fragmentary olenellids and bradoriids but no additional specimens of *A*? *davisi* (J. S. Peel, unpublished observation).

The conspicuous granulated ornamentation on the cephalon of A? davisi is also seen in Atops rupertensis Jell, Jago & Gehling, 1992 from the Lower Cambrian of the Flinders Ranges, Australia. The glabella in the Greenland species is narrower and more parallel sided in contrast to the wide, rounded glabella of At. rupestris but the S1 glabellar furrows in both species are inclined back and similar. A? davisi has well-developed paired pleural spines not reported in the Australian species.

Alacephalus occurs within the Bigotinid faunal province of the Lower Cambrian (Pillola 1990) in the Altai-Sayan region of Siberia whereas North Greenland is characterised by olenellid trilobites. If the tentative assignment of the North Greenland specimen to Alacephalus can be maintained, it provides one of very few records of trilobites common to the two provinces.

Fig. 81. Alacephalus? davisi Lane & Rushton, 1992. Uppermost Buen Formation. Damaged complete specimen, holotype, MGUH 21143 from GGU collection 319544. 1, sculpture of right fixigena, x 4. 2, dorsal view, x 1.5. 3, imprint of ventral(?) surface of hypostome; the strong oblique furrows are due to the posterolateral margin of the hypostome resting against the S1 lateral glabellar furrows, x 3. 4, axial rings of thoracic segments 1-3, x 3. 5, paired left pleural spines of segments 8-11, x 3 (photographs by P. D. Lane from Lane & Rushton 1992).



Occurrence in North Greenland. – Upper Buen Formation, (Fig. 3, locality 7). Age: Early Cambrian, *Olenellus* Zone.

Genus Kleptothule Budd, 1995

Type species. – *Kleptothule rasmusseni* Budd, 1995 from the Lower Cambrian Buen Formation of North Greenland (Fig. 3, locality 5).

Kleptothule rasmusseni Budd, 1995

Fig. 82



Fig. 82. *Kleptothule rasmusseni* Budd, 1995. Lowermost Buen Formation. Dorsal view of damaged complete specimen from the Sirius Passet fauna, holotype, MGUH 22355 from GGU collection 340103, x 4, (photograph by G. E. Budd).

1995 Kleptothule rasmusseni Budd, p. 4, figs 2-9

Figured material. – Damaged complete specimen, MGUH 22355 from GGU collection 340103).

Discussion. – *Kleptothule rasmusseni* is known from at least 60 specimens from the Sirius Passet fauna from the lower part of the Buen Formation where it is associated with *Buenellus higginsi* Blaker, 1988. This elongate, lightly mineralised, trilobite-like arthropod contains about 27 segments in the thorax and a further 20 in the caudal region. Budd (1995) compared *Kleptothule* to the olenellinid trilobites but no precise placement is attempted here.

Occurrence in North Greenland. – Lower Buen Formation, (Fig. 3, locality 5). Age: Early Cambrian, "*Nevadella*" Zone.

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