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Agnostoid trilobites and biostratigraphy of the middle Cambrian Manuels River Formation in the type locality at Conception Bay South, Newfoundland, Canada

Gutachter: Prof. Dr. Peter Bengtson
PD Dr. Christina Ifrim

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AGNOSTOID TRILOBITES AND BIOSTRATIGRAPHY OF THE MIDDLE CAMBRIAN MANUELS RIVER FORMATION IN THE TYPE LOCALITY AT CONCEPTION BAY SOUTH, NEWFOUNDLAND, CANADA

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Abstract

Agnostoid trilobites from the type locality of the middle Cambrian (Series 3, Drumian) Manuels River Formation, Newfoundland, Canada, are described systematically. The fauna consists of 1408 specimens, collected bed-by-bed. The taxa are assigned to the suborders Agnostina and Eodiscina, families Peronopsidae, Ptychagnostidae, Condylopygidae and Eodiscidae, genera *Peronopsis* Hawle and Corda, 1847, *Hypagnostus* Jaekel, 1909, *Ptychagnostus* Jaekel, 1909, *Tomagnostus* Howell, 1935, *Pleuroctenium* Hawle and Corda, 1847, and *Eodiscus* Hartt *in* Walcott, 1884, and the species *Peronopsis fallax* (Linnarsson, 1869), *Peronopsis scutalis* (Hicks, 1872), *Hypagnostus parvifrons* (Linnarsson, 1869), *Ptychagnostus punctuosus* (Angelin, 1851), *Ptychagnostus affinis* (Brøgger, 1879), *Ptychagnostus atavus* (Tullberg, 1880), *Tomagnostus fissus* (Lundgren *in* Linnarsson, 1879), *Tomagnostus perrugatus* (Grönwall, 1902), *Pleuroctenium granulatum* (Barrande, 1846) and *Eodiscus punctatus* (Salter, 1864b). The faunal assemblage is subdivided from base to top into five interval zones, *viz*. *Peronopsis scutalis*, *Tomagnostus fissus*, *Ptychagnostus atavus*, *Ptychagnostus affinis* and *Ptychagnostus punctuosus* zones. The *Ptychagnostus punctuosus* Zone can be compared regionally and globally. The entire fauna is comparable to that of Baltica and Greenland, which suggests geographic proximity during the middle Cambrian. *Pleuroctenium granulatum* is endemic to Avalonia and Baltica.

Keywords: Agnostida, trilobites, biostratigraphy, palaeobiogeography, middle Cambrian, Series 3, Drumian, Manuels River Formation, Avalonia, Newfoundland, Canada.

Kurzfassung

Agnostoide Trilobiten der Typuslokalität der mittelkambischen (Serie 3, Drumium) Manuels-River-Formation, Neufundland, Kanada, werden systematisch beschrieben. Die Schicht-für-Schicht gesammelte Fauna besteht aus 1408 Exemplaren. Die Taxa werden den Unterordnungen Agnostina und Eodiscina, Familien Peronopsidae, Ptychagnostidae, Condylopygidae und Eodiscidae, Gattungen *Peronopsis* Hawle and Corda, 1847, *Hypagnostus* Jaekel, 1909, *Ptychagnostus* Jaekel, 1909, *Tomagnostus* Howell, 1935, *Pleuroctenium* Hawle and Corda, 1847, und *Eodiscus* Hartt *in* Walcott, 1884, und den Arten *Peronopsis fallax* (Linnarsson, 1869), *Peronopsis scutalis* (Hicks, 1872), *Hypagnostus parvifrons* (Linnarsson, 1869), *Ptychagnostus punctuosus* (Angelin, 1851), *Ptychagnostus affinis* (Brøgger, 1879), *Ptychagnostus atavus* (Tullberg, 1880), *Tomagnostus fissus* (Lundgren *in* Linnarsson, 1879), *Tomagnostus perrugatus* (Grönwall, 1902), *Pleuroctenium granulatum* (Barrande, 1846) und *Eodiscus punctatus* (Salter, 1864b) zugeordnet. Von der Basis bis zum Top wird die Faunenabfolge in fünf Intervall-Zonen untergliedert, und zwar der *Peronopsis scutalis*-, *Tomagnostus fissus*-, *Ptychagnostus atavus*-, *Ptychagnostus affinis*- und der *Ptychagnostus punctuosus*-Zone. Die *Ptychagnostus punctuosus*-Zone kann regional und global nachvollzogen werden. Die gesamte Fauna ist mit der von Baltika und Grönland vergleichbar, was eine geographische Nähe während des Mittelkambriums nahelegt. *Pleuroctenium granulatum* ist endemisch auf Avalonia und Baltika.

Schlüsselwörter: Agnostida, Trilobiten, Biostratigraphie, Paläobiogeographie, Mittelkambrium, Serie 3, Drumium, Manuels-River-Formation, Avalonia, Neufundland, Kanada.

Contents

1. **Introduction**

Detailed palaeontological studies of the middle Cambrian Manuels River Formation at its type locality, Conception Bay South, Newfoundland, Canada, were carried out by Howell (1925) and Hutchinson (1962). Howell (1925) studied the succession bed-by-bed and Hutchinson (1962) carried out systematic descriptions of the trilobite fauna. Previous studies of the formation were mainly focused on descriptions of trilobites of the orders Ptychopariida and Redlichiida (e.g., Poulsen and Anderson, 1975; Bergström and Levi-Setti, 1978). Other studies dealt with microfossils, such as acritarchs and “small shelly fossils” (Martin and Dean, 1988; Hildenbrand, 2012). In order to revise and refine the trilobite systematics and biostratigraphy, the author spent seven months (July–September 2012, July–August 2013, July–August 2014) at the type locality of the formation, sampling agnostoid trilobites from the highly fossiliferous shales.

Agnostoid trilobites are of particular interest for biostratigraphic purpose, as they evolved rapidly and widely. They occur abundantly in the middle middle Cambrian to the middle upper Cambrian (Drumian, Series 3) (Geyer and Shergold, 2000; Peng and Robison, 2000). So, they are used for middle Cambrian biostratigraphy and for precise palaeobiogeographic reconstructions.

The Manuels River Formation consists mainly of grey to black shales, with interbedded calcareous concretions and minor volcanic-ash layers. The sediments were deposited on the microcontinent Avalonia, located in temperate southern latitudes, near the northern margin of the supercontinent Gondwana. The deposition occurred in a marine, shallow, dysoxic environment, in a mainly warm semi-humid climatic setting, with sudden changes to semi-arid conditions (Austermann, 2016).

Based on detailed bed-by-bed collecting from the succession of the type locality of the formation exposed along Manuels River, a revised agnostoid trilobite systematics has been achieved. The results give new insights into the biostratigraphy and biogeography of Avalonia compared to other continents (e.g., Baltica and Laurentia) during the middle Cambrian.

1.1. Historical review

Jukes (1842) was the first to describe the sedimentary rocks of the Conception Bay South area including the shales at Manuels River. He described these as “Upper Slate Formation”. He did not mention any fossils and an age determination was not given. Murray (1869) described several successions of the Conception Bay South area. He observed syenitic gneiss, conglomerates, shales and limestones of different successions along the Manuels River valley. He (Murray, 1869) also reported on the sediments along the river and assigned them to the Lower Silurian, but did not describe any fossils from Manuels River. In the upper part of the shales at Branch, St. Mary’s Bay, Newfoundland, he mentioned the occurrence of the trilobite *Paradoxides bennetti*.

In 1874, T. C. Weston collected trilobites from the shales of Manuels River. Whiteaves (1878) published and summarized the fossil finds of Weston and reported on the similarity of the trilobite fauna from Manuels River and St. John, New Brunswick. He listed

- *Agnostus acadicus* Hartt *in* Dawson, 1868, in the present study suggested to be a “*nomen dubium*” (see Chapter *Ptychagnostus fallax*)
- *Microdiscus punctatus* Salter, 1864b, currently named *Eodiscus punctatus* (Salter, 1864b)
- *Microdiscus dawsoni* Hartt *in* Dawson, 1868, currently named *Dawsonia dawsoni* (Hartt *in* Dawson, 1868)
- *Conocephalites tener* Hartt *in* Dawson, 1868, currently named *Badulesia tenera* (Hartt *in* Dawson, 1868)
- *Conocephalites baileyi* Hartt *in* Dawson, 1868, currently named *Bailiella baileyi* (Hartt *in* Dawson, 1868)

Several studies were published between 1881 and 1900 about the palaeontology, stratigraphy and classification of middle Cambrian sedimentary rocks in North America and Atlantic Canada (Murray and Howley, 1881; Matthew, 1886, 1896, 1899; Walcott, 1888a, 1888b, 1889, 1900; Marcou, 1890; Weston, 1896).

Howell (1925) presented the first detailed description of the succession exposed along Manuels River. He described grey to black mudstones in several beds (bed numbers 36–125) with the associated fossil content. The fossils are mainly agnostoid, redlichiid and ptychopariid trilobites but also brachiopods and hyoliths. He described and illustrated eight new defined species in detail (six of the Order Agnostida, two of the Order Ptychopariida and one of the Order Redlichiida). Howell (1925) defined the Long Pond and Kelligrew Brook formations and introduced the two biozones *Paradoxides hicksi* and *Paradoxides davidis* zones.

Later, Hutchinson (1962) studied several successions of the formation in the southeastern part of Newfoundland and proposed the name Manuels River Formation for Howell’s (1925) beds 36–125. He designated the succession on the west bank of Manuels River as the type locality because it is best exposed, best accessible and mainly comformable. Hutchinson (1962) revised and supplemented the systematic work of Howell (1925). His detailed work included illustrations and descriptions of the entire trilobite fauna.

The study of Poulsen and Anderson (1975) presented a biostratigraphy of mainly agnostoid trilobites of the upper Manuels River Fomation and the lower Elliot Cove Formation at Manuels River and Random Island. The middle to upper Cambrian successions in southeastern Newfoundland showed similar faunas to Scandinavia and England e.g., *Ptychagnostus punctuosus*, *Lejopyge laevigata* and *Andrarina costata*.

Bergström and Levi-Setti (1978) studied the upper part of the Manuels River Formation bed-by-bed on the east side of the river. They described two subspecies of *Paradoxides davidis* Salter, 1863 (*P. davidis trapezopyge* and *P. davidis intermedius*) from different intervals of the formation. By means of semi-quantitative x-ray anlaysis and thin sectioning Bergström and Levi-Setti (1978) proposed a coincidence of depositional discontinuites of the Manuels River Formation.

The first study of microfossils was done by Martin and Dean (1988), who described in their biostratigraphic study acritarchs and trilobites zones from Manuels River and Random Island. Several illustrations and descriptions of the species in the systematic part were presented. The proposed acritarch biozones were supplemented by the trilobite zones *Tomagnostus fissus* and *Ptychagnostus atavus* zones, *Hypagnostus parvifrons* Zone and the *Ptychagnostus punctuosus* Zone of the Manuels River Formation (Martin and Dean, 1988).

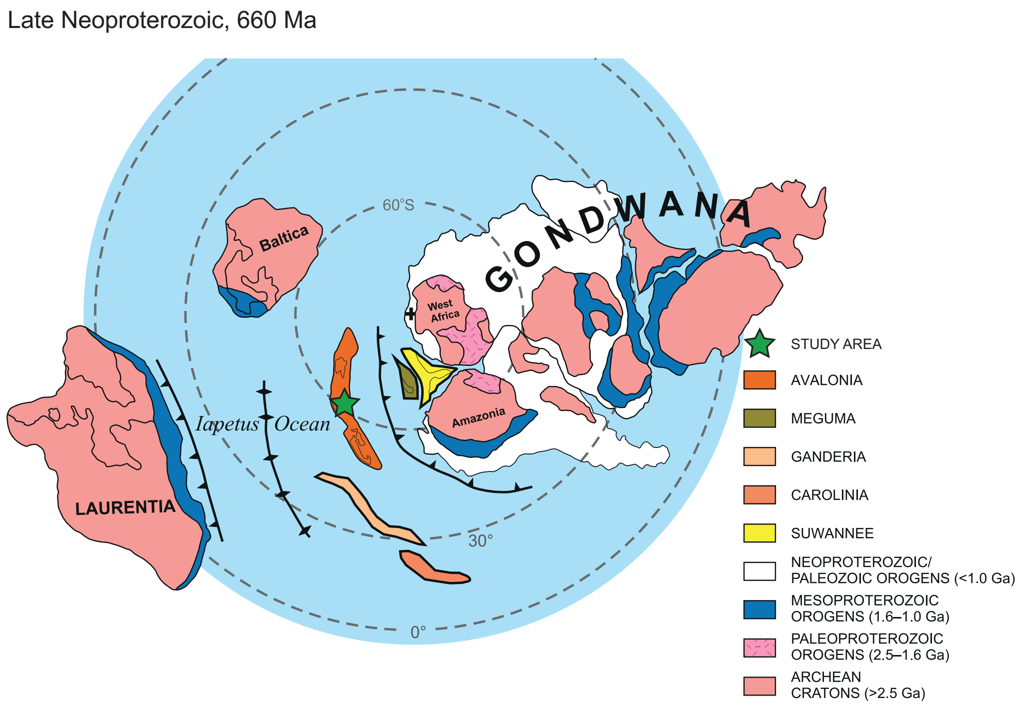
Hildenbrand (2012) studied calcareous and clayey concretions and their fossil content from the Manuels River Fomation at its type locality. The concretions were dissolved and three-dimensional “small shelly fossils” of trilobites, brachiopods, hexactinellide sponge spicules and problematica were described. In addition, conference contributions of Hildenbrand *et al.* (2012) and Austermann *et al.* (2012) deal with the small shelly fossils of the succession. Vetter (2012) studied the interbedded volcanic ash layers, and Malang (2015) and Wetzel (2015) carried out a geological mapping of the west and east banks of the Manuels River valley.

The present study was carried out in a close collaboration with Austermann (2016), who discusses in detail the depositional environment and the palaeogeography of the Manuels River Formation at its type locality.

In addition to the publications mentioned above, several field-trip guides, field books, conference contributions, unpublished theses and illustrated books deal with the palaeontology and/or the stratigraphy of the Manuels River Formation at its type locality: Nautiyal (1966); Brückner (1978); Anderson (1987); Landing and Benus (1988); Levi-Setti (1993, 2014); Milner (1995); Boyce (1988, 2001, 2006); Landing and Westrop (1998a,b) and Fletcher (2006).

1.2. Palaeogeography of Avalonia

The eastern part of Newfoundland was in the early Paleozoic part of the microcontinent Avalonia, which is considered to be the largest terrane of the peri-Gondwanan realm (Pollock *et al.*, 2012). Avalonia is named after the Avalon Peninsula, which is located in the south-eastern part of Newfoundland (Cocks *et al.*, 1997). In the Neoproterozoic, Avalonia was situated between the Iapetus Ocean in the north and the supercontinent Gondwana in the south (Fig. 1). Cocks *et al.* (1997) postulated a connection of Avalonia and Gondwana on the basis of similarities in their trilobite faunas. Throughout the Neoproterozoic and Cambrian, Gondwana and Avalonia were located near the South Pole (McKerrow *et al.*, 1992; Keppie, 1993; Cocks and Torsvik, 2006).



Late Neoproterozoic, 660 Ma

Fig. 1: Late Neoproterozoic palaeogeography (based on Pollock *et al.*, 2012 and Austermann, 2016, with modifications).

During the Neoproterozoic, Avalonia went through different stages of evolution characterised by volcanic-arc and rift developments (Nance *et al.*, 2002), with the corresponding deposition of volcanic rocks and sediments (O'Brien *et al.*, 1996; Murphy *et al.*, 1999; Pollock *et al.*, 2012). These processes were caused by the rifting of the Iapetus Ocean and the subduction of the oceanic crust beneath the supercontinent Gondwana at 635–570 Ma (Nance *et al.*, 2002). Thus, Avalonia was part of the subducting plate that moved towards Gondwana. Murphy and Nance (1989) argued that there is no evidence of an orogenic collision and Murphy *et al.* (1999) envisaged a ridge-trench collision and progressive development of a dextral continental transform fault. This dextral continental transform fault caused a lateral movement from Avalonia along the margin of Gondwana, which proceeded during the Cambrian (542–485 Ma) (Fig. 2). Thus, the connection of Avalonia and Gondwana persisted (Nance *et al.*, 2002; van Staal *et al.*, 1998). During the closure of the Iapetus Ocean and the opening of the Rheic Ocean in the early Ordovician (Fig. 3), Avalonia began separating from Gondwana and moved in northwards towards Laurentia. Early Ordovician trilobite and brachiopod faunas of Avalonia are conspicuosly different from those of Baltica and Laurentia, which corroborates the distances between these three continents (Cocks *et al.*, 1997). In the Silurian, Avalonia drifted further north (Fig. 4), and the Iapetus Ocean closed (Pollock *et al.*, 2012). Cocks *et al.* (1997) and Pollock *et al.* (2012) suggested a dispersal barrier resulting from the different shelly faunas of Gondwana and Avalonia as a result of the widening developed Rheic Ocean in between the continents.

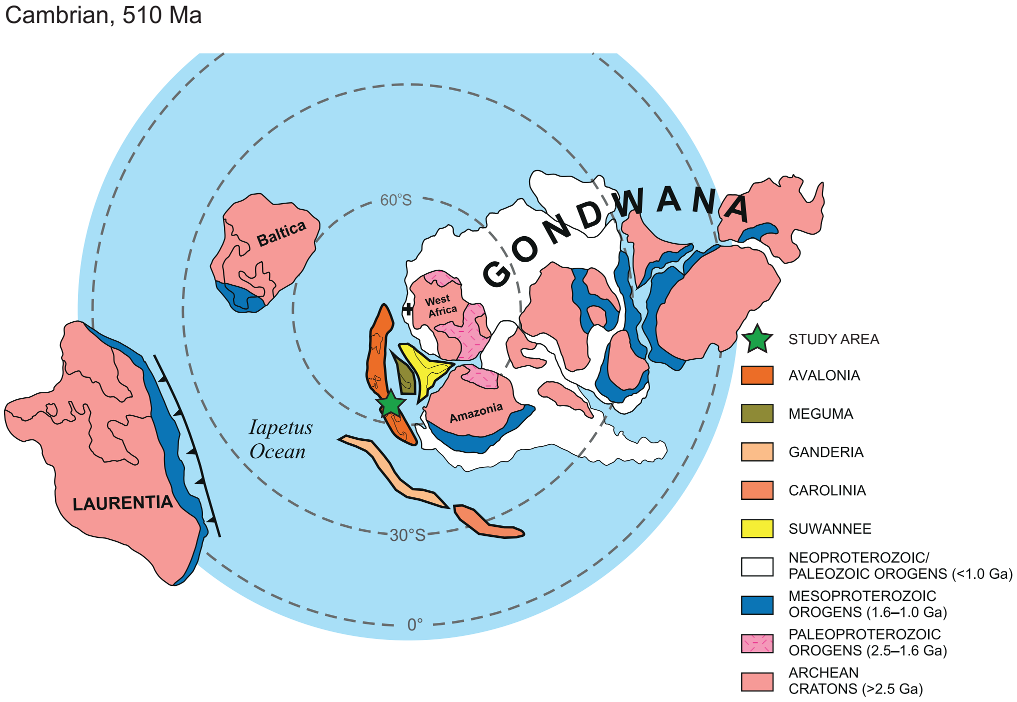


Fig. 2: Cambrian palaeogeography (based on Pollock *et al.*, 2012, with modifications).

In the Devonian, Avalonia merged with Laurentia and in the late Devonian–Carboniferous, both collided with Gondwana as part of the formation of the supercontinent Pangaea (Pollock *et al.*, 2012) (Fig. 5). The opening of the Atlantic Ocean during the Cretaceous led to the breakup of the Avalonian complex, geographically in East and West

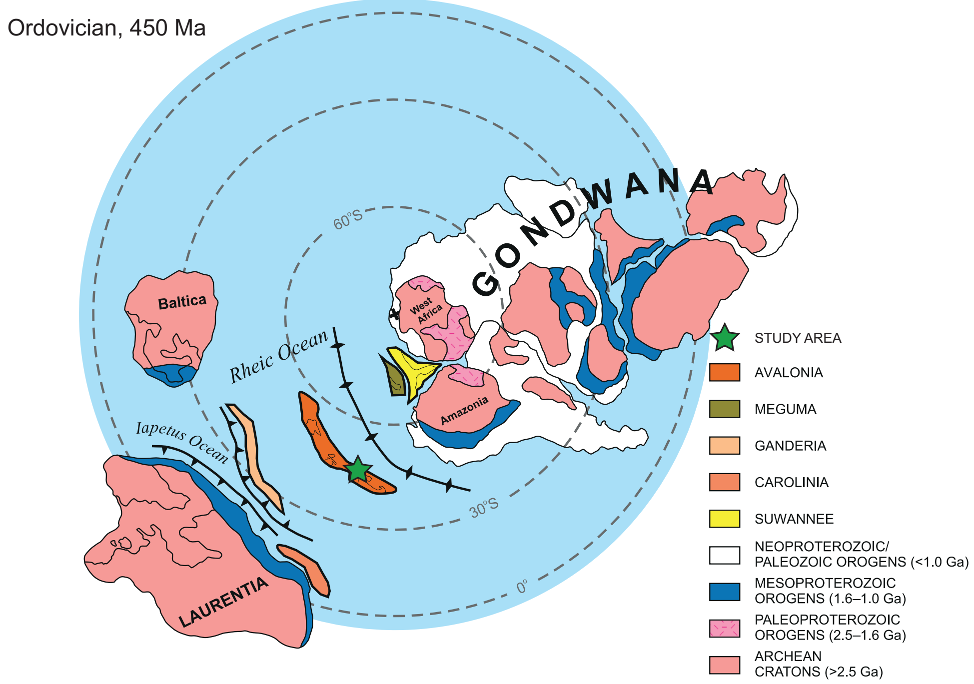


Fig. 3: Ordovician palaeogeography (based on Pollock *et al.*, 2012, with modifications).

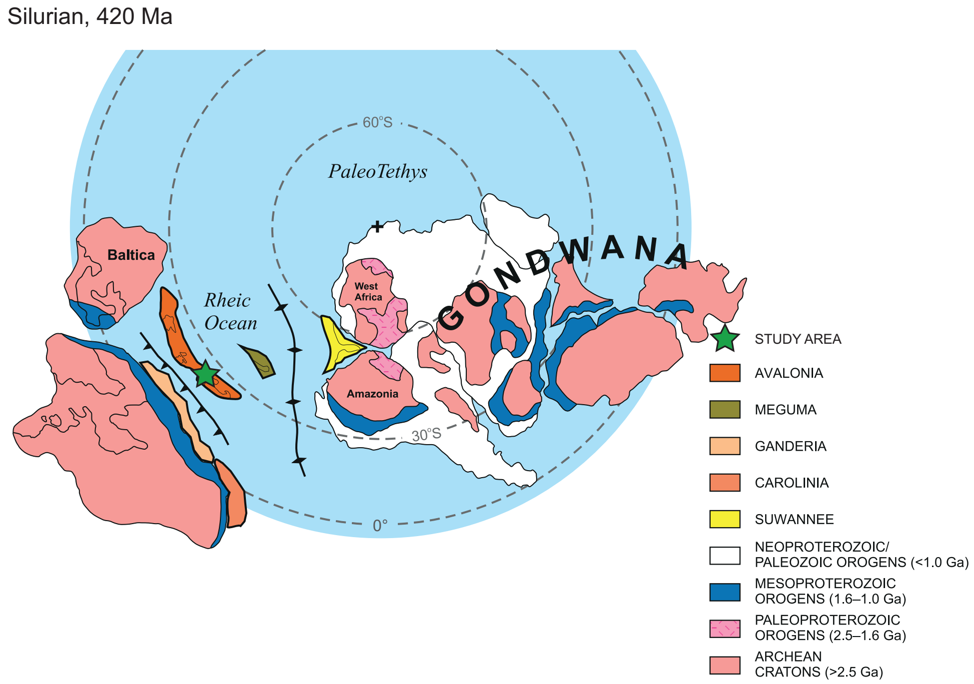


Fig. 4: Silurian palaeogeography (based on Pollock *et al.*, 2012, with modifications).

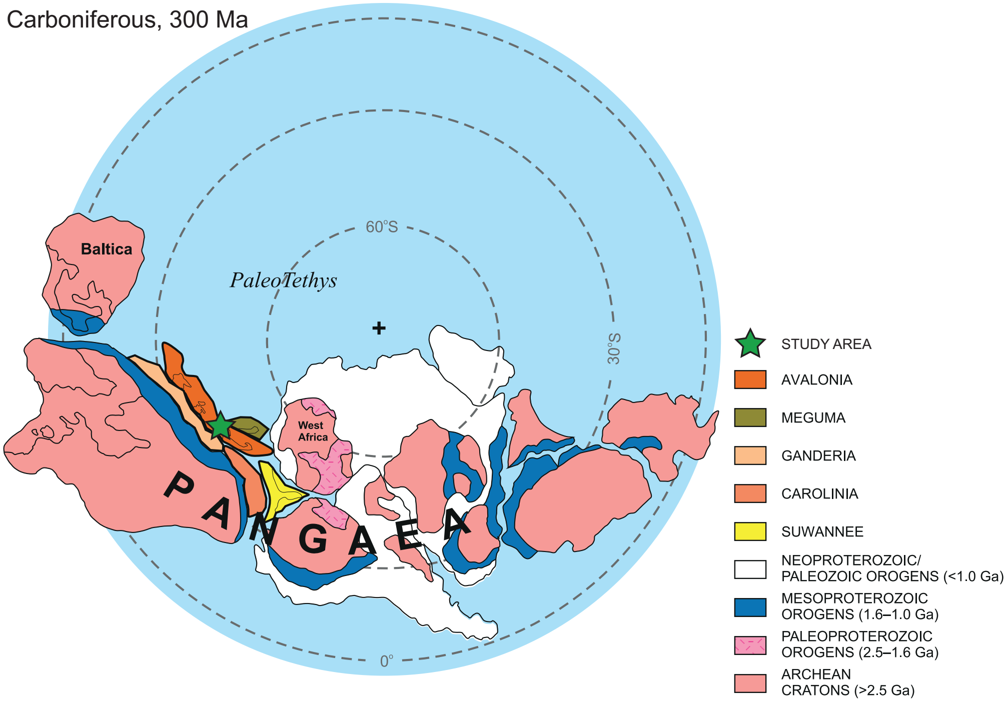


Fig. 5: Carboniferous palaeogeography (based on Pollock *et al.*, 2012, with modifications).

Avalonia. Today, East Avalonia includes southern England, Wales, southeast Ireland, Belgium, northern Netherlands, northern Germany and parts of the Bohemian massif and the West-Sudets (Cocks *et al.*, 1997; Cocks and Torsvik, 2002; Nance *et al.*, 2002). West Avalonia consists of the Avalon and Burin Peninsula of southeastern Newfoundland, Cape Breton Island, Nova Scotia, New Brunswick, eastern Massachusetts, Connecticut, New Hampshire, Maine and Rhode Island (Fig. 6) (e.g., O'Brien *et al.*, 1996; Cocks *et al.*, 1997; Hibbard *et al.*, 2007).

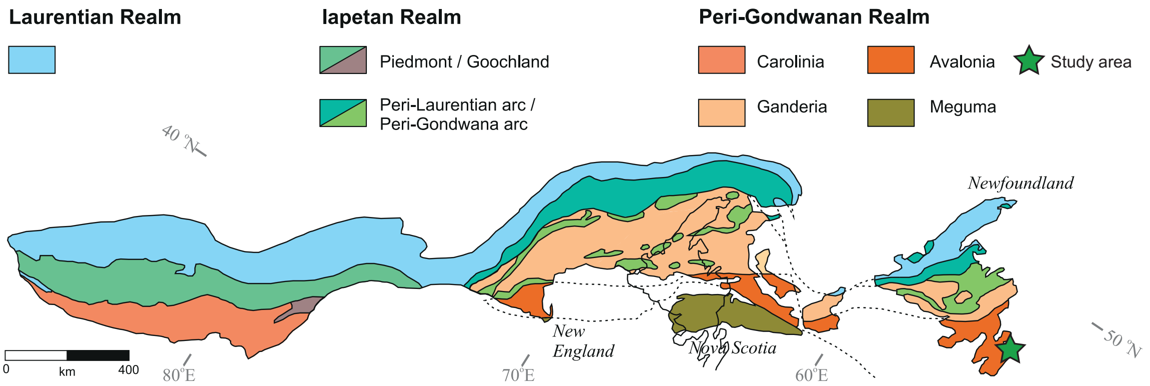


Fig. 6: Peri-Gondwanan realm with locations of western parts of Avalonia. The green star marks the study area (based on Pollock *et al.*, 2012, with modifications).

1.3. Regional geology

The Cambrian succession exposed along Manuels River overlies disconformably the Neoproterozoic magmatic rocks (e.g., rhyoliths, granites and dacites) of the Holyrood Horst (see King 1988, 1990; Malang, 2015; Wetzel 2015). The Horst forms a solid basement for the overlying sediments and is bordered by two main faults (Topsail and Brigus faults) on the western and eastern margins (Rose, 1952; King, 1988, 1990) (Fig. 7). On the entire Avalon Peninsula, the Cambrian successions consist of shallow-marine to deep-marine sediments with only minor faults (Hutchinson, 1952, 1962; Fletcher 1972, 2006; Landing, 2004).

At Manuels River the lower Cambrian Brigus Formation overlies nonconformably the Neoproterozoic rocks (Anderson, 1987; Hutchinson, 1962). The base of the formation consists of a basal conglomerate, overlain by mudstones. Thin-bedded limestones are intercalated in the formation (Anderson, 1987; Landing and Westrop, 1998a). The top of the Brigus Formation is erosional. The base of the disconformably overlying lower middle Cambrian Chamberlain's Brook Formation consists of manganese-rich sedimentary rocks, followed by greenish mudstones with intercalated thin-bedded limestones (Landing and Benus, 1988) and interbedded carbonate concretions. A conformable contact with a thin volcanic ash layer as marker horizon forms the base of the middle Cambrian Manuels River Formation, consisting of black shales with interbedded thin volcanic ash layers and carbonate concretions (Howell, 1925; Hutchinson, 1962; Austermann, 2016). The contact with the overlying Elliot Cove formation is disconformable, caused by a regression-transgression sequence. The base of the Elliot Cove formation is formed by a coarse sandstone to conglomerate (Howell, 1925; Hutchinson, 1962; Poulsen and Anderson, 1975; Austermann, 2016). The Elliot Cove formation consists of shales with interbedded carbonate concretions (Hutchinson, 1962; Malang, 2015). Malang (2015) proposed a coarsening-upward trend in this formation, as he observed sandstones in the upper part. The top of the Elliot Cove formation is possibly exposed in the Conception Bay area, between the estuary of the Manuels River and Bell Island. The Ordovician of the island consists of mainly siltstones and sandstones of the Bell Island and Wabana Groups (King, 1988).

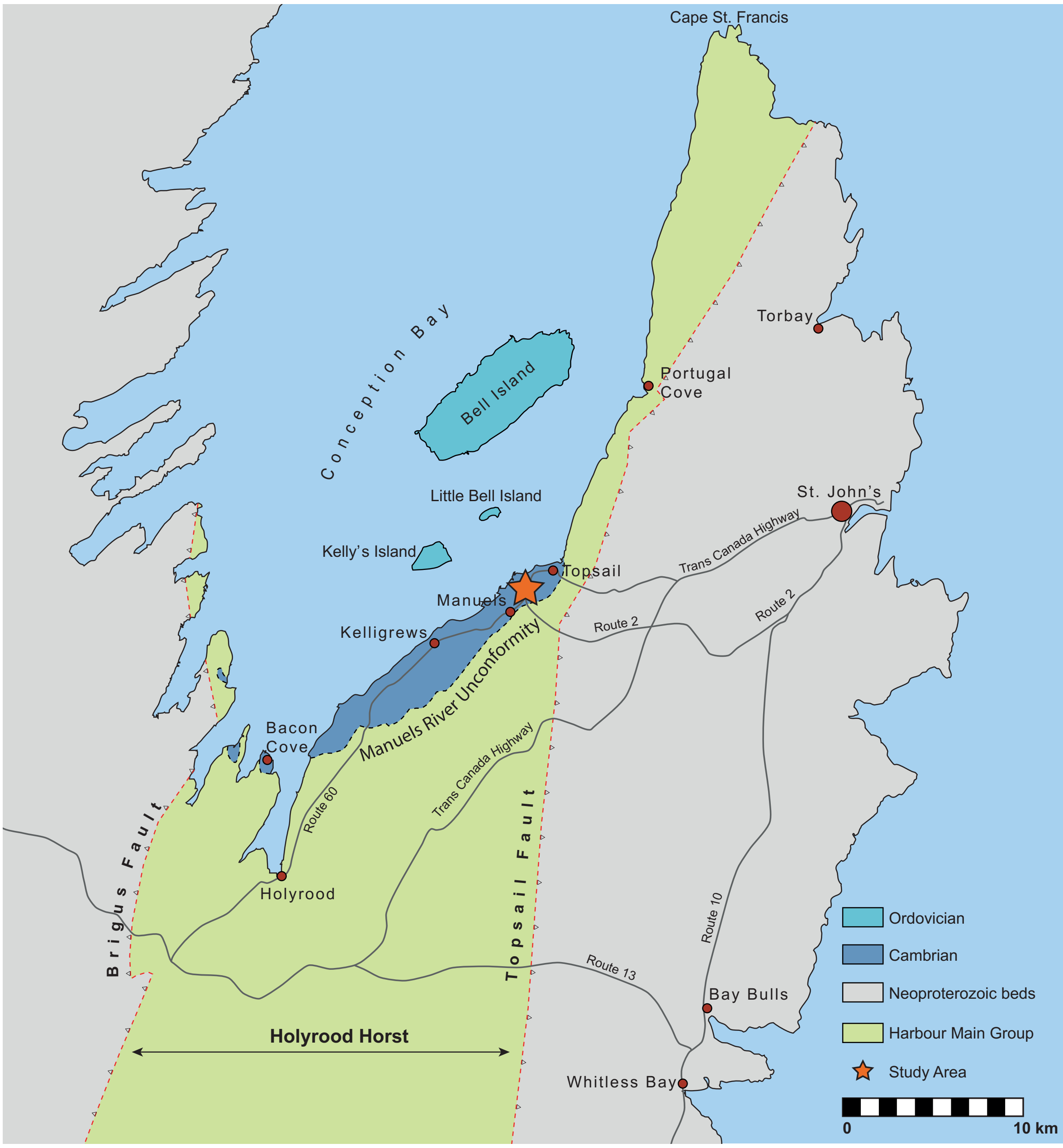


Fig. 7: Geological map of the Conecption Bay area, southeastern part of Newfoundland, showing the study area located on the Holyrood Horst (based on King, 1990, with modifications).

1.4. Study area

The 10-km-long Manuels River flows from the south-eastern inland of the Avalon Peninsula to the north-west into Conception Bay, Newfoundland, Canada (Fig. 8). The estuary is located at the community of Manuels, Conception Bay South, on the south-eastern coast of the bay. The entrance to the Manuels River valley is situated next to the Newfoundland Route 60, 21 km from St. John's, the capital city of Newfoundland.

The Manuels River Hibernia Interpretation Centre is the starting point for foot trails down the Manuels River valley (Fig. 9). After 400 m down the valley in north-west direction, on the west bank of the river the type locality of the Manuels River Formation is exposed (47.52512°N, -52.95119°E). The base of the Manuels River Formation lies approximately 4 m above mean-sea-level (ASML) and extends to the valley slope. The entire Manuels

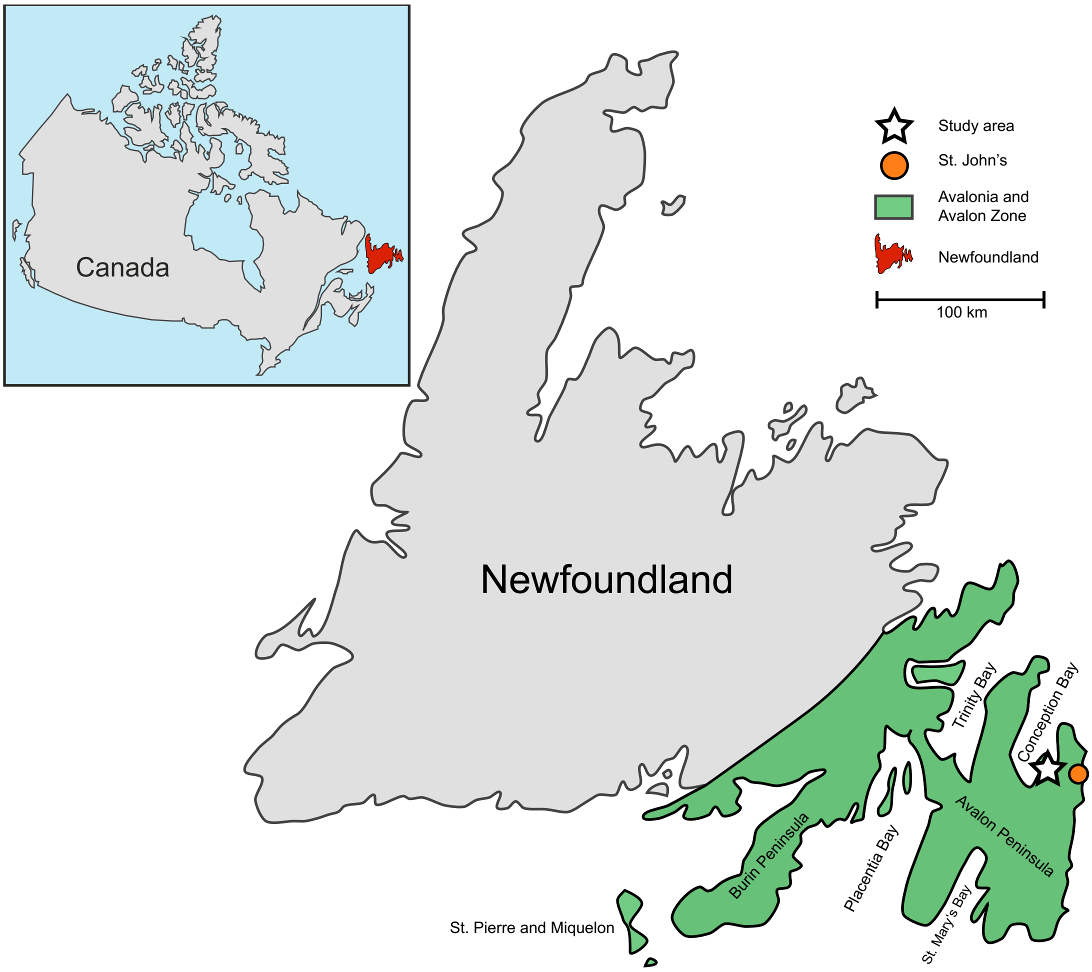


Fig. 8: Map of Newfoundland, showing Avalonia with several bays, the capital St. John's and the study area at Manuels River, Conception Bay.

River valley is protected by the Newfoundland and Labrador law, Regulation 67/11 “Palaeontological Resource Regulations under the Historic Resources Act”.

Fig. 9: Map of the downstream part of Manuels River located in the community Manuels, Conception Bay South. The Manuels River Trail leads to the type locality of the Manuels River Formation (white star).

1.5. Manuels River Formation

1.5.1. **Definition and lithology**

The middle Cambrian Manuels River Formation is widely exposed in the eastern part of Newfoundland, e.g., on Random Island, Trinity Bay, the eastern area of Conception Bay, the western part of St. Mary's Bay, Placentia Bay, the southern Burin Peninsula, on the French islands of St. Pierre and Miquelon and on Cape Breton Island (Fig. 8). The formation was defined by Hutchinson (1962), based on the detailed studies of Howell (1925), who proposed the Long Pond (11.28 m in thickness) and Kelligrew Brook formations (9.45 m in thickness). In Hutchinson's view, the exposures along Manuels River are the best completely exposed and easy of access and he selected a section at Manuels River as the type locality. The thickness of the formation varies across the Avalon Peninsula, from 20.73 m (68 feet) (Howell, 1925) at the type locality to 29–33 m (95–110 feet) at Highland Cove, Trinity Bay and Fosters Point on Random Island (Hutchinson, 1962).

The base of the formation is a 5–13 cm thick, soft, white bentonite bed, described as a "metabentonite" (Fletcher, 1972) and later revised by Vetter (2012) as a K-Bentonite, which is also exposed at Trinity Bay and St. Mary's Bay (Hutchinson, 1962; Fletcher, 2006). The formation consists mainly of fine clastic grey to black mudstones with intercalated limestones (Howell, 1925; Hutchinson, 1962; Fletcher 1972, 2006). In addition, volcanic sediments, such as tuff beds, occur in the upper part of the formation in the area around St. Mary's Bay (Fletcher, 1972, 2006). The top of the formation is described by Howell (1925) as a conglomerate (bed 125) and by Hutchinson (1962) as a thick-bedded shale with grey nodules to a mainly silty shale with black nodules. The overlying "Elliot Cove Group" consists also of shales (Howell, 1925; Hutchinson, 1962).

1.5.2. **Fossil content**

The shales of the Manuels River Formation are highly fossiliferous. The main fossil groups are trilobites of the orders Agnostida, Ptychopariida and Redlichiida with fluctuating diversities and stratigraphic ranges (Howell, 1925; Hutchinson, 1962; Poulsen and Anderson, 1975; Bergström and Levi-Setti, 1978; Martin and Dean, 1988). Species of Ptychopariida, e.g., *Agraulos socialis,* occur mainly in the lower half of the formation (Howell, 1925) (beds 36–87). By contrast, species of the Order Redlichiida, e.g., *Paradoxides hicksi* and *Paradoxides davidis,* appear at different heights throughout the whole succession (Howell, 1925; Hutchinson, 1962). For detailed systematic studies of Ptychopariida and Redlichiida see Hutchinson (1962), Bergström and Levi-Setti (1978) and Martin and Dean (1988).

Other macrofossils are brachiopods and hyoliths, both occurring at several levels. The brachiopods appear abundantly at the base of the succession (beds 37–41), with minor occurrences in beds 41 and 101 (see Howell, 1925). Several specimens of undetermined hyoliths were also described from the succession (Howell, 1925). In addition, several of the calcareous concretions contain small shelly fossils, e.g., brachiopods, scattered trilobites, spicules of hexactinellid sponges and problematica (Hildenbrand, 2012). Other microfossils of the succession are acritarchs, reported on by Martin and Dean (1988).

1.5.3. **Local biostratigraphy**

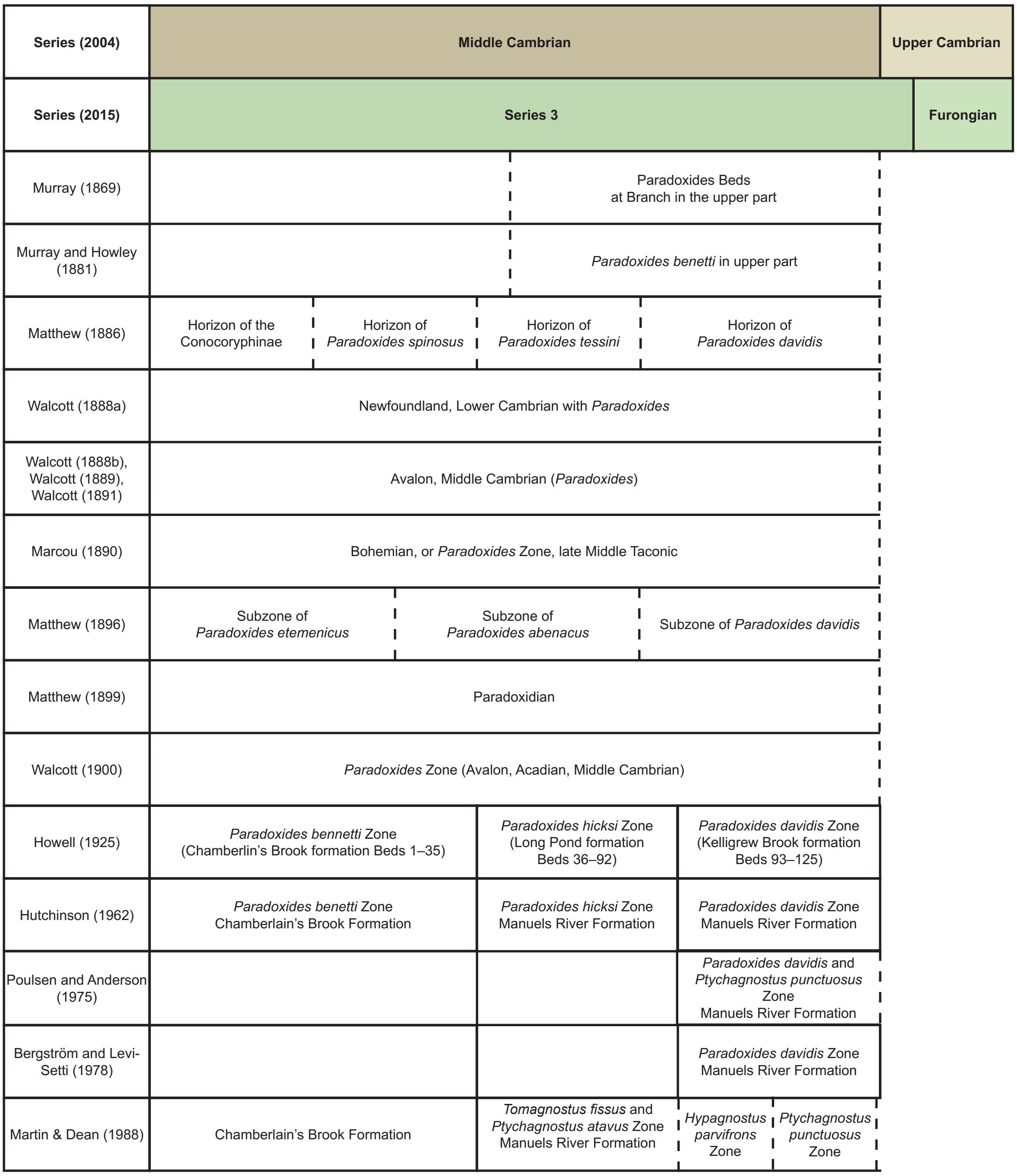
The history of biostratigraphic zonation of the middle Cambrian Manuels River Formation in the area of its type locality is illustrated in Fig. 10. The pre-Howell (1925) authors focused more on the subdivison of the Conception Bay area, Newfoundland, and the North American continent in general, rather than on the detailed biostratigraphy at Manuels River.

The first detailed zonation of Howell (1925) at the type locality of the formation is based on the trilobites. He divided the shales of the Manuels valley into three formations with associated biozones. The lowest zone (*Paradoxides bennetti* Zone*)* corresponds to the Chamberlin's Brook formation (beds 1–35), which is today defined as the Chamberlains's Brook Formation.

Howell (1925) described the *Paradoxides hicksi* Zone (beds 36–92) of the Long Pond formation and the *Paradoxides davidis* Zone (beds 93–125) of the Kelligrew Brook formation on the basis of lithological and faunal changes within the succession. The lower, *Paradoxides hicksi* Zone, comprises the species *Paradoxides hicksi* and abundant agnostoid trilobites. The upper, *Paradoxides davidis* Zone, is characterised by the species *Paradoxides davidis* Salter, 1863 and abundant agnostoid trilobites (Howell, 1925; Hutchinson, 1962).

Hutchinson (1962) confirmed the local biostratigraphic zones of the middle middle Cambrian to upper middle Cambrian proposed by Howell (1925). Nevertheless Hutchinson (1962) considered the Long Pond formation and the Kelligrew Brook formation described by Howell (1925) local members of the Manuels River Formation. At other outcrops of the formation in Newfoundland these lithological subdivisions are not distinguishable. Hutchinson (1962) subdivided the Manuels River Formation in two biozones based on Howell's (1925) suggestion.

Poulsen and Anderson (1975) defined biozones of the upper Manuels River Formation and the lower Elliot Cove formation using agnostoid trilobites. They collected *Ptychagnostus punctuosus* (Angelin, 1851) in the upper part of the formation, from the biozone with the same name, correlating the global biostratigraphy of the upper middle Cambrian (see Chapter *Ptychagnostus punctuosus*). At the base of the overlying Elliot Cove formation, *Lejopyge*



<table>
<tr><td>Series (2004)</td><td colspan="8">Middle Cambrian</td><td colspan="2">Upper Cambrian</td></tr>
<tr><td>Series (2015)</td><td colspan="9">Series 3</td><td>Furongian</td></tr>
<tr><td>Murray (1869)</td><td colspan="4"></td><td colspan="4">Paradoxides Beds
at Branch in the upper part</td><td colspan="2"></td></tr>
<tr><td>Murray and Howley (1881)</td><td colspan="4"></td><td colspan="4"><i>Paradoxides benetti</i> in upper part</td><td colspan="2"></td></tr>
<tr><td>Matthew (1886)</td><td>Horizon of the Conocoryphinae</td><td colspan="2">Horizon of <i>Paradoxides spinosus</i></td><td colspan="2">Horizon of <i>Paradoxides tessini</i></td><td colspan="3">Horizon of <i>Paradoxides davidis</i></td><td colspan="2"></td></tr>
<tr><td>Walcott (1888a)</td><td colspan="8">Newfoundland, Lower Cambrian with <i>Paradoxides</i></td><td colspan="2"></td></tr>
<tr><td>Walcott (1888b),
Walcott (1889),
Walcott (1891)</td><td colspan="8">Avalon, Middle Cambrian (<i>Paradoxides</i>)</td><td colspan="2"></td></tr>
<tr><td>Marcou (1890)</td><td colspan="8">Bohemian, or <i>Paradoxides</i> Zone, late Middle Taconic</td><td colspan="2"></td></tr>
<tr><td>Matthew (1896)</td><td colspan="2">Subzone of <i>Paradoxides etemenicus</i></td><td colspan="3">Subzone of <i>Paradoxides abenacus</i></td><td colspan="3">Subzone of <i>Paradoxides davidis</i></td><td colspan="2"></td></tr>
<tr><td>Matthew (1899)</td><td colspan="8">Paradoxidian</td><td colspan="2"></td></tr>
<tr><td>Walcott (1900)</td><td colspan="8"><i>Paradoxides</i> Zone (Avalon, Acadian, Middle Cambrian)</td><td colspan="2"></td></tr>
<tr><td>Howell (1925)</td><td colspan="3"><i>Paradoxides bennetti</i> Zone
(Chamberlin's Brook formation Beds 1–35)</td><td colspan="3"><i>Paradoxides hicksi</i> Zone
(Long Pond formation Beds 36–92)</td><td colspan="2"><i>Paradoxides davidis</i> Zone
(Kelligrew Brook formation Beds 93–125)</td><td colspan="2"></td></tr>
<tr><td>Hutchinson (1962)</td><td colspan="3"><i>Paradoxides benetti</i> Zone
Chamberlain's Brook Formation</td><td colspan="3"><i>Paradoxides hicksi</i> Zone
Manuels River Formation</td><td colspan="2"><i>Paradoxides davidis</i> Zone
Manuels River Formation</td><td colspan="2"></td></tr>
<tr><td>Poulsen and Anderson (1975)</td><td colspan="3"></td><td colspan="3"></td><td colspan="2"><i>Paradoxides davidis</i> and <i>Ptychagnostus punctuosus</i> Zone
Manuels River Formation</td><td colspan="2"></td></tr>
<tr><td>Bergström and Levi-Setti (1978)</td><td colspan="3"></td><td colspan="3"></td><td colspan="2"><i>Paradoxides davidis</i> Zone
Manuels River Formation</td><td colspan="2"></td></tr>
<tr><td>Martin & Dean (1988)</td><td colspan="3">Chamberlain's Brook Formation</td><td colspan="3"><i>Tomagnostus fissus</i> and <i>Ptychagnostus atavus</i> Zone
Manuels River Formation</td><td><i>Hypagnostus parvifrons</i> Zone</td><td><i>Ptychagnostus punctuosus</i> Zone</td><td colspan="2"></td></tr>
</table>

Fig. 10: The Biostratigraphy with different biozones of several studies of the Manuels River Formation at Manuels River, Newfoundland.

laevigata and *Peronopsis insignis* were found. Nowadays, the FAD of *Lejopyge laevigata* defines the Drumian Stage of Series 3 (Peng *et al.*, 2012).

Bergström and Levi-Setti (1978) presented a biozonation of the upper part of the Manuels River Fomation and followed the concept of *Paradoxides davidis* of Howell (1925) and Hutchinson (1962). Martin and Dean (1988) studied for the first time acritarchs and trilobites and integrated these taxa for a biozonation of the formation on both sides of the valley. They redefined the older biozones and divided the formation in three biozones *Tomagnostus fissus* and *Ptychagnostus atavus* zones, *Hypagnostus parvifrons* Zone (with lower and upper limits uncertain) and *Ptychagnostus punctuosus* Zone. The conglomerate of Howell's (1925) bed 125 is taken as the basal bed of the Elliot Cove formation by Martin and Dean (1988) and Austermann (2016).

2. **Material and methods**

The material described in this study was collected together with G. Austermann, Heidelberg University (see Austermann, 2016). The agnostoid trilobites were collected bed-by-bed, at a one-cm-resolution, from the entire succession exposed at the type locality of the Manuels River Formation, Newfoundland, Canada. Most of the fossils occur in grey to black shales, with a few specimens in interbedded calcareous concretions. Currently, the collection is on loan to Heidelberg University from The Rooms Corporation of Newfoundland and Labrador, Provincal Museum Division, Natural History Unit, St. John's, Newfoundland, Canada (NFM).

The described specimens were supplemented with study of type specimens from the collections of Hutchinson (1962) and Martin and Dean (1988). These latter collections are housed in the Geological Survey of Canada, Ottawa, Canada (GSC).

In this study, the synonymy lists comprise mainly peer-reviewed studies published in the Latin alphabet, with a few exceptions (e.g. Russian). Further, all studies used herein were available for the author by interlibrary loan. Unpublished theses and field guides are only cited with the permission of the author. In general, only studies with a comprehensible description of the particular species and/or pictures are cited in the synonymy lists.

The specimens were measured with a 0.1 mm accuracy by using a venier calliper. For photography, a Leitz binocular and camera with ring-light illumination was used with a directed LED light from the upper left. The illustrated photographs were calibrated with Adobe Photoshop.

2.1. Chronostratigraphy

The Cambrian System was traditionally subdivided into three series, lower, middle and upper, according to Sedgwick's (1852). In this concept, the first appearance of trilobites marked the base of the lower Cambrian. After fifteen decades of discussion (see Peng and Babcock, 2011; Peng *et al.*, 2012) the three-series concept was replaced in 2004 by a four-series subdivision by the International Subcommisson on Cambrian Stratigraphy (ISCS) (Peng, 2004; Peng and Babcock, 2011; Peng *et al.*, 2012). The base of the Terreneuvian, the base of the Cambrian System, is now characterised by the first appearance datum (FAD) of the trace fossil *Trichophycus pedum* and a significant change in trace-fossil associations (Peng *et al.*, 2012). The global stratotype section and Point (GSSP) for the base of the Cambrian System was designated at Fortune Head, Burin Peninsula, Newfoundland (Brasier *et al.*, 1994). The Terreneuvian is characterised by the absence of trilobites, whereas the Series 2–Furongian successions commonly contain trilobites. Because they often fulfill the requirements of good guide fossils, such as relatively short stratigraphic ranges, cosmopolitan distribution in open-marine facies and abundant occurrence the FADs of selected trilobites have been or are being proposed for the definition of the eight stages of the Series 2–Furongian (see Babcock *et al.*, 2005; Peng and Babcock, 2005; Peng *et al.*, 2012, Cohen *et al.*, 2013).

The Cambrian System of West Avalonia is subdivided into the regional units Placentian, Branchian, Acadian and Merionethian. The succession here studied was deposited during the Acadian, which ranges from the base of Series 3 to the upper but not topmost Series 3, more precisely from the base of Stage 5 to the middle Guzhangian (Peng *et al.*, 2012). The base of the Drumian, forming the middle part of Series 3 is lies at the FAD of the cosmopolitan *Ptychagnostus atavus* (Babcock *et al.*, 2007). The base of the following Guzhangian (uppermost Series 3) lies at the FAD of *Lejopyge laevigata* (Peng *et al.*, 2012).

International Stratigraphic Chart 2015/01			**Regional Units**	**Boundary Horizons (GSSPs) or provisional Stratigraphic Tie Points**
System	**Series**	**Stage**	**Avalonia**	
Ordovician	Lower	Tremadocian	Tremadocian	⊥ *Iapetognathus fluctivagus* (GSSP)
Cambrian	Furongian	Stage 10	Merionethian	⊥ *Lotagnostus americanus*
		Jiangshanian		⊥ *Agnostotes orientalis* (GSSP)
		Paibian		⊥ *Glyptagnostus reticulatus* (GSSP)
	Series 3	Guzhangian	Acadian	⊥ *Lejopyge laevigata* (GSSP)
		Drumian		⊥ *Ptychagnostus atavus* (GSSP)
		Stage 5		⊥ *Oryctocephalus indicus* / *Ovatoryctocara granulata*
	Series 2	Stage 4	Branchian	? *Olenellus*, *Redlichia*, *Judomia*, or *Bergeroniellus*
		Stage 3	Placentian	? Trilobites
	Terreneuvian	Stage 2		? *Watsonella crosbyi* or *Aldanella attleborensis*
		Fortunian		⊥ *Trichophycus pedum* (GSSP)
Ediacaran				

Fig. 11: West Avalonian chronostratigraphic chart showing regional correlations of the Cambrian system with their corresponding GSSPs and FADs, respectively (based on Babcock *et al.*, 2005; Peng *et al.*, 2012 and Cohen *et al.*, 2013, with modifications).

As shown in Chapter Manuels River Formation, most studies of the Manuels River succession were published using the three-series subdivision of the Cambrian. This concept, although now informal, is considered useful in Avalonian aspects (e.g., Fletcher, 2006; Landing *et al.*, 2006). Also, the agnostoid biozonation of the Drumian, which is used for global correlation, cannot yet be applied to Avalonia. To faciliate correlations and comparisons with previous studies, the traditional terms (e.g., middle Cambrian) are used here in an informal sense (Fig. 11).

2.2. Terminology

Most morphological terms used in this study were described by Shergold *et al.* (1990, p. 18, fig. 2) and Whittington *et al.* (1997, p. 10, fig. 6) (Figs. 12, 13). Supplementary Robison (1982) is followed here, who described the types of basal lobes and the shapes of the pygidial axis (Figs. 14, 15). In the past decades, the terms for the description of agnostids have changed and synonyms introduced. For example, the term “cheek” was used by Howell (1925), Westergård (1946) and others, whereas here “genae” is used, following Whittington *et al.* (1997).

The entire terminology used in the present study is additionally described below.

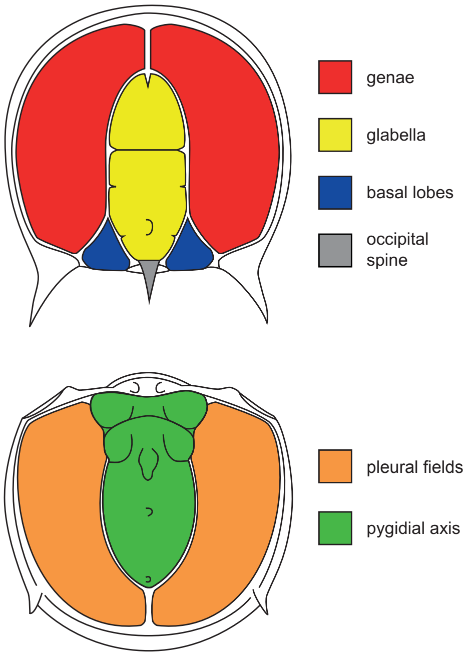


Fig. 12: Visualisation of morphological terms for cephalon and pygidium (based on Shergold *et al.* (1990) and Whittington *et al.* (1997), with modifications).

gena. Two genae are developed on the cephalon, to the left and right side of the glabella and margined by the cephalic border furrow.

glabella. The glabella consists of the anterior glabellar lobe and the posterior glabellar lobe and is situated longitudinally in the middle of the cephalon.

occipital spine. Spine (typical for Eodiscidae) extending the posterior end of the glabella and run posteriorly to the thoracic segments.

pleural fields (pygidial). Two pleural fields on the pygidium, situated on the left and right side of the pygidial axis and margined by the pygidial border furrow, in some cases divided by the a median postaxial furrow.

preglabellar field. The area on the cephalic genae between the anterior glabellar lobe and the cephalic border furrow, in some cases divided by a median preglabellar furrow.

pygidial axis. Axis composed of the anteroaxis and posteraxis, situated longitudinally in the middle of the pygidium.

pygidial collar. A single crescentic-shaped ridge on the pygidial border.

scrobiculation. Radiating furrows, variable in strength, situated on the cephalic genae. The furrows start on the genae next to the cephalic border and end on the genae.

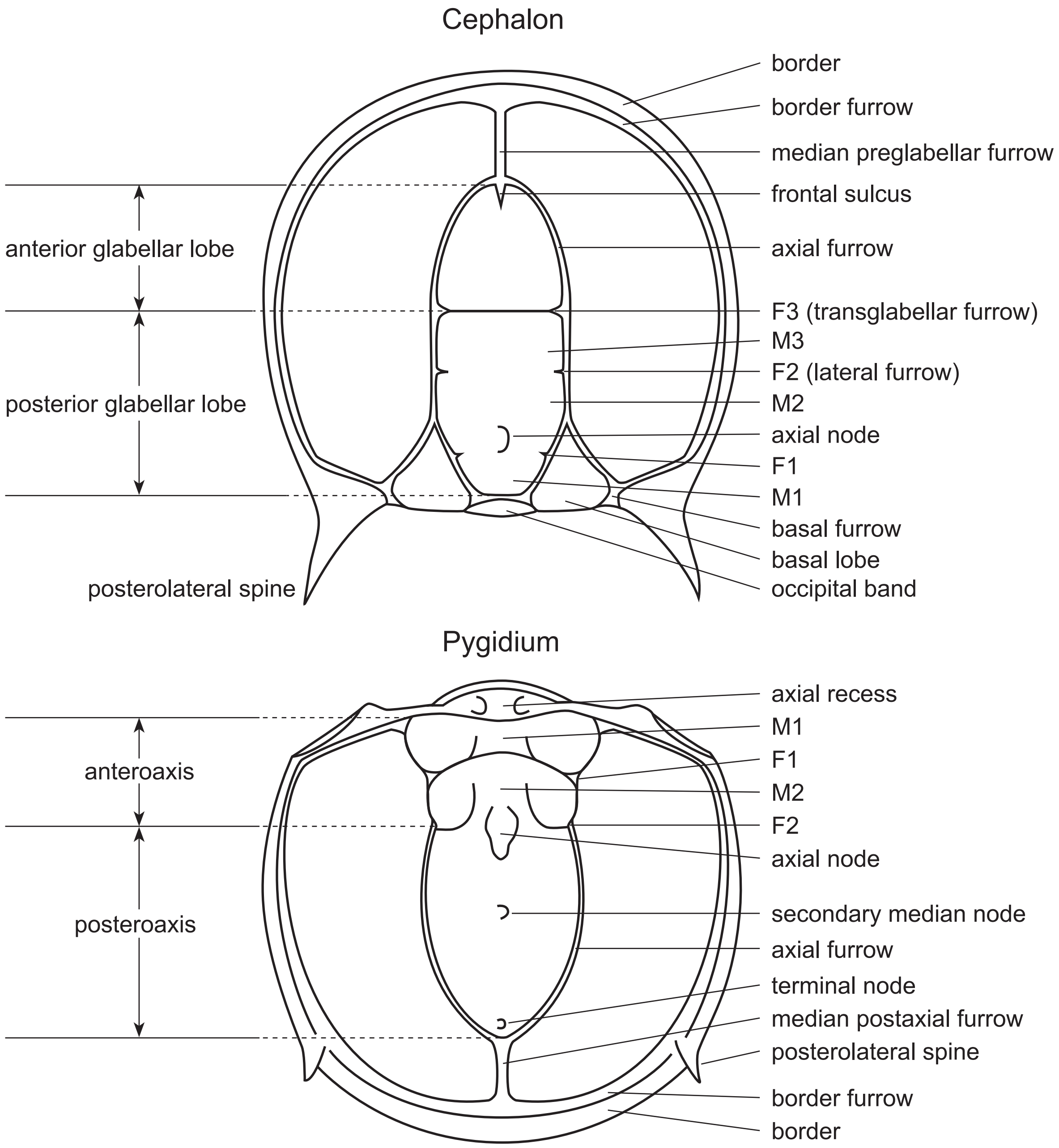


Fig. 13: Morphological terms for describing the external surface of Agnostida, Cephalon and Pygidium (based on Shergold *et al.* (1990) and Whittington *et al.* (1997), with modifications).

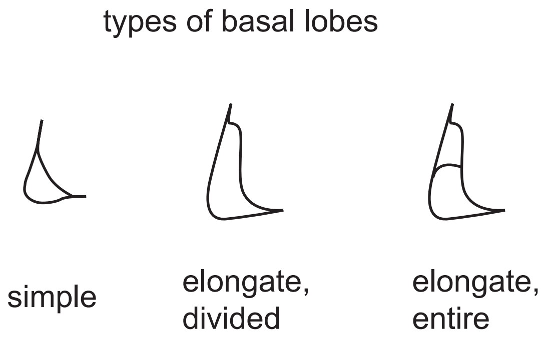


Fig. 14: Different types of basal lobes of agnostoid trilobites (based on Robison (1982), with modifications).

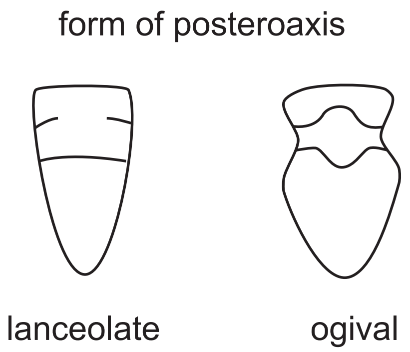


Fig. 15: Different forms of the pygidial posteroaxis of agnostoid trilobites (based on Robison (1982), with modifications).

In the synonymy lists, abbreviations and symbols are used for detailed nomenclatural decisions. For this purpose, Matthews (1973), Bengtson (1988) and Becker (2001) are followed. All used abbreviations and symbols are placed before the year.

?	the identification is uncertain, possibly a synonym
pars	only a part of the material is assigned to the species
non	explicitly not assigned to the species
v	*vidimus*, the specimens of the cited study were checked

3. Systematic palaeontology

Phylum Arthropoda Siebold and Stannius, 1846
Class Trilobita Walch, 1771
Order Agnostida Salter, 1864a
Suborder Agnostina Salter, 1864a
Superfamily Agnostoidea M'Coy, 1849
Family Peronopsidae Westergård, 1936
Genus *Peronopsis* Hawle and Corda, 1847

Type species. *Battus integer* Beyrich, 1845, by original designation.

Diagnosis. Cephalon nonscrobiculate and smooth; median preglabellar furrow absent; subquadrate to semiovate anterior glabellar lobe; F3 furrow straight; axial node on posterior glabellar lobe near F2 furrow; basal lobes simple; pygidial axis with F1 and F2 furrows weak to absent; axis with weakly developed transverse depression at midlength (based on Robison, 1994; Whittington *et al.*, 1997, with modifications).

Synonyms. *Mesospheniscus* Hawle and Corda, 1847; *Mesagnostus* Jaekel, 1909.

Remarks. *Peronposis* Hawle and Corda, 1847, includes the oldest described and figured agnostoids with containing many genera of the middle Cambrian (Laurie, 1990; Naimark, 2012). More than 100 species have been assigned to this genus (Rushton, 1979; Robison, 1994, 1995; Weidner and Nielsen, 2014). The morphological characters vary during ontogeny and within population, which leds to a complex taxonomic subdivison of *Peronopsis* (Robison, 1982; Naimark, 2012).

Because of these conditions there are frequent discussions about synonyms. *Acadagnostus* Kobayashi, 1939, is one of the consistently discussed synonyms (e.g. Rushton, 1979; Laurie, 1990; Robison, 1994, 1995; Whittington *et al.*, 1997). Originally the genus was described by Kobayashi (1939) as having a pygidial lanceolate axis and a pygidial median postaxial furrow and lacking a pair of pygidial posterolateral spines. By contrast, *Peronopsis* is very variable in the pygidial median postaxial furrow as well as the occurrence of spines. Whittington *et al.* (1997) presented a diagnosis of *Acadagnostus* which indicates pygidial spines and the pygidial axis never reaching the border furrow. Because of the absence of a description or discussion about the retype of the diagnosis, it is here suggested to follow the original description of the genus, so *Acadagnostus* is here not considered a synonym of *Peronopsis*.

Some species of *Euagnostus* Whitehouse, 1936, have a median preglabellar furrow, which is not found *Peronopsis*. Therefore, Høyberget and Bruton (2008) suggested to exclude this genus from the synonymy list of *Peronopsis*, a view followed here.

Peronopsis fallax (Linnarsson, 1869)

(Text-figs. 16 A–C)

1869 *Agnostus fallax* n. sp. Linnarsson, pp. 81–82, pl. 2, figs. 54–55.
pars 1879 *Agnostus fallax*, Linrs.; Brøgger, pp. 64–65, pl. 6, fig. 1 (not 1 a).
? 1879 *Agnostus fallax* Linrs.; Linnarsson, pp. 22–23, pl. 2, fig. 33.
? 1880 *Agnostus fallax* Linrs. *forma typica*; Tullberg, p. 31, pl. 2, fig. 22.
pars 1886 *Agnostus acadicus*, Hartt; Matthew, p. 70, pl. 7, fig. 5 a (not 5 b).
1886 *Agnostus vir*, n. sp. Matthew, pp. 69–70, pl. 7 fig. 3.
1886 *Agnostus vir*, var. *concinnus* Matthew, p. 70, pl. 7, figs. 4 a–c.
1892 *Agnostus vir* Matthew, 1885; Vogdes, pp. 388–389, pl. 10, fig. 14.
1892 *Agnostus vir* var. *concinnus* Matthew, 1885; Vogdes, p. 389, pl. 9, fig. 13.
pars 1896 *Agnostus fallax* Linrs.; Matthew, pp. 214–215, pl. 15, fig. 8 a (not 8 b).
1896 *Agnostus fallax* var. *vir.* Matthew, pp. 215–216, pl. 15, fig. 6.
? 1896 *Agnostus fallax* var. *concinnus* Matthew, p. 216, pl. 15, figs. 7 a–c.
1906 *Agnostus fallax*, Linnarsson; Lake, pp. 20–21, pl. 2, fig. 12.
1906 *Agnostus fallax*, Linnarsson, nov. var. *laiwuensis* Lorenz, pp. 82–84, pl. 4, figs. 7 a–8 b; pl. 5, figs. 8–9.
pars 1910 *Agnostus acadicus* Hartt; Grabau and Shimer, p. 256, fig. 1543 a (not 1543 b).
1911 *Agnostus fallax* Linnarsson; Cobbold, p. 291, pl. 25, figs. 17 a–18 b.
1915 *Agnostus fallax* Linnarsson; Illing, p. 416, pl. 31, figs. 12–15.
1925 *Agnostus clarae*, n. sp. Howell, pp. 74–75, pl. 3, fig. 1.
non 1929 *Agnostus fallax* Linrs.; Strand, p. 346–347, pl. 1, fig. 19.
1936 *Peronopsis fallax* (Linnarsson, 1869); Westergård, pp. 28–29, pl. 1, figs. 9–15.
1946 *Peronopsis fallax* (Linnarsson, 1869); Westergård, p. 37, pl. 2, figs. 18–24.
? 1952 *Peronopsis* cf. *fallax* (Linnarsson) var. *concinnus* (Matthew); Hutchinson, p. 69, pl. 1, figs. 2–3.

? 1952 *Peronopsis fallax* (Linnarsson, 1869); Henningsmoen, p. 15, pl. 2, fig. 5.

1961 *Peronopsis fallax fallax* (Linnarsson 1869); Sdzuy, pp. 522–523, pl. 1, figs. 18–22.

1961 *Peronopsis* cf. *fallax* (Linnarsson 1869); Sdzuy, pp. 522–523, pl. 1, figs. 23–25.

1962 *Peronopsis fallax* (Linnarsson) subsp. *P. depressa* Westergård; Hutchinson, p. 70, pl. 5, figs. 8–11.

1972 *Peronopsis* cf. *P. fallax* (Linnarsson); Palmer and Gatehouse, p. 10, pl. 4, figs. 6–7.

1979 *Peronopsis fallax* (Linnarsson); Öpik, pp. 54–55, pl. 4, figs. 4–7.

1979 *Peronopsis fallax depressa* Westergaard 1946; Rushton, p. 50, fig. 3 B.

1981 *Peronopsis fallax* (Linnarsson 1869); Gil Cid, p. 33, pl. 1, fig. 3.

1981 *Peronopsis fallax fallax* (Linnarsson 1869); Gil Cid, p. 28, pl. 1, figs. 1–2.

1982 *Peronopsis fallax* (Linnarsson, 1869) aff. *minor* (Brögger, 1878); Dean, pp. 5–8, figs. 3 a–d, 4–5.

pars 1982 *Peronopsis fallax* (Linnarsson, 1869); Egorova *et al.*, pp. 66–67, pl. 2, fig. 1; pl. 5, fig. 6; pl. 9, figs. 3–4; pl. 13, fig. 6; pl. 18, fig. 7; pl. 19, fig. 3; pl. 41, figs. 3–5, 11; pl. 51, figs. 15–16 (not pl. 10, fig. 3; pl. 62, figs. 5–6).

1982 *Peronopsis fallax* (Linnarsson); Robison, pp. 152–156, pl. 6, figs. 5–8.

1989 *Peronopsis fallax* (Linnarsson, 1869); Young and Ludvigsen, pp. 11–12, pl. 1, figs. 16–20.

1990 *Axagnostus fallax* (Linnarsson 1869); Laurie, pp. 319–322, figs. 1 A–D, F, H–J.

1990 *Peronopsis* sp. indet. Laurie, pp. 320–321, figs. 1 E, G.

pars 1990 *Peronopsis fallax* (Linnarsson, 1869); Samson *et al.*, p. 1466, fig. 5 A (not 5 B).

1994 *Peronopsis fallax* (Linnarsson, 1869); Robison, pp. 43–44, figs. 19. 3–4.

1994 *Axagnostus fallax* (Linnarsson 1869); Rudolph, pp. 145–146, pl. 9, figs. 6–7.

1995 *Peronopsis acadica* Hartt (in Dawson, 1868); Robison, pp. 302–305, figs. 1. 1–3.

1997 *Acadagnostus fallax* (Linnarsson); Whittington *et al.*, p. 363, figs. 230.8 a–b.

2003 *Peronopsis fallax fallax* (Linnarsson, 1869); Axheimer and Ahlberg, p. 144, figs. 4 H–I.

2006 *Peronopsis fallax* (Linnarsson, 1869); Fletcher, pp. 66–67, fig. 40.

2008 *Peronopsis fallax* (Linnarsson 1869); Høyberget and Bruton, pp. 28–29, pl. 3, figs. A–H.

? 2009 *Acadagnostus fallax* (Linnarsson, 1869); Weidner and Nielsen, p. 265, figs. 15 B–C.

2014 *Acadagnostus acadicus* (Hartt in Dawson, 1868); Weidner and Nielsen, pp. 38–39, figs. 32 A–C.

Diagnosis. Cephalon and pygidium subquadrate to subcircular; cephalic and pygidial border furrows widely developed; pygidial axial node large and elongate; pygidial pair of posterolateral spines (based on Robison, 1982; Høyberget and Bruton, 2008, with modifications).

Lectotype. Specimen no. SGU 4716, Swedish Geological Survey, Uppsala, Sweden, by subsequent designation of Laurie (1990, p. 320, fig. 1 B), originally figured by Westergård (1946).

Material. Five complete specimens, 141 cephala and 131 pygidia (NFM F-998–F-1274) from the middle part of the Manuels River Formation type locality (5.91–16.41 m), Conception Bay South, Newfoundland, Canada.

Description. The specimens are mainly well preserved. The complete specimens are varying from 3.5 to 7.2 mm in length. The size of the cephala varies from 2.4 to 4.9 mm in width and from 2.2 to 4.5 mm in length. The size of the pygidia varies from 1.6 to 5.3 mm in width and from 1.2 to 4.8 mm in length. Some of the specimens show yellow colour from the pyrite contained in the shales.

All cephala and pygidia are subquadrate to subcircular. The characteristic wide border furrows are well developed. In some smaller cephala the border furrow is narrower. The cephalic axial node is small but visible. There is a larger variation in the pygidia of the specimens. The axis varies from ogival and tapered to broader. Some specimens show a tapered end reaching the border furrow, or the axis is long without a contact to the furrow. A median postaxial furrow is in some specimens visible. Some pygidia show a weakly transverse depression in midlength of the axis. All pygidia show a pair of posterolateral spines.

Discussion. *Peronopsis fallax* (Linnarsson, 1869) shows many morphological variations and is a long ranging species (Robison, 1982; Høyberget and Bruton, 2008). The cephala are subquadrate to subcircular. The width of the cephala and pygidia increases during ontogeny.

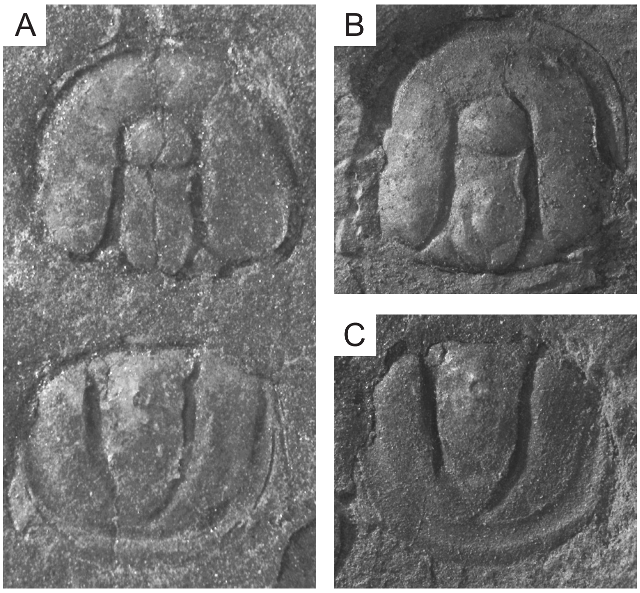


Fig. 16: *Peronopsis fallax* (Linnarsson, 1869); **A**, complete specimens (NFM F-998), ×10; **B**, cephalon (NFM F-999), ×10; **C**, pygidium (NFM F-1000), ×10.

This is for example, visible in characters such as border furrows, which are getting wider from meraspis to the holaspis stage (Robison, 1995).

The length of the pygidial axis varies from ending in the postaxial area near the border furrow, or with contact to the median postaxial furrow, or reaching the border furrow. Høyberget and Bruton (2008) described this tendency by the stratigraphic occurrence of the species and by intraspecific variations. Stratigraphically older specimens, from the early middle Cambrian, are reaching the border furrow while later occuring specimens (*Ptychagnostus atavus* Zone) show a contact to the median postaxial furrow. In addition, the median postaxial furrow gets fainter or absent during advanced ontogeny (Robison, 1982).

Due to these variations the systematic position of *P. fallax* is still controversial discussed (e.g., Hutchinson, 1952; Gil Cid, 1981; Laurie, 1990; Robison, 1994, 1995; Høyberget and Bruton, 2008; Weidner and Nielsen, 2009, 2014).

Robison (1995) and Weidner and Nielsen (2014) assigned *P. fallax* (Linnarsson, 1869) as a junior subjective synonym of *Agnostus acadicus* Hartt *in* Dawson, 1868. Robison (1995) described in detail, that the type material has to be seen critical, because Hartt *in* Dawson (1868) mentioned uncertainty about the togetherness of the cephalon and pygidium. In the first description Hartt *in* Dawson (1868) mentioned the uncertainty if they belong to the same species, because they were sampled separately and he only found one specimens. Öpik (1979) and Robison (1995) suggested to assign the questionably type pygidium of Hartt to *Hypagnostus parvifrons* (Linnarsson, 1869) (see Chapter *Hypagnostus parvifrons*). The illustrated specimens in Dawson (1868) shows a spineless pygidium, which is not characteristic for *P. fallax*. In addition, Matthew (1896) and Robison (1995) collected both at the same horizon in the St. John's region and found many specimens of *A. acadicus* with pygidial spines rather than nonspinose pygidia. The cephalon sampled by Hartt *in* Dawson (1868) is in Robison's (1995) view still the holotype of *A. acadicus* and therefore a senior subjective synonym of *P. fallax*. It is now type species of *Acadagnostus*, Kobayashi, 1939, as described in Whittington *et al.* (1997) (see Chapter *Peronopsis*). In the present study it is followed the suggestion of Høyberget and Bruton (2008), that Hartt's species should be regarded as a "*nomen dubium*" because the type material is to be seen doubtful and is not reviewable.

Beside this discussion *P. fallax* is distinguished from the closely related species *Peronopsis ferox* (Tullberg, 1880) mainly by characteristics of the pygidia. *P. ferox* has a broader and shorter pygidial axis than *P. fallax*, thus the postaxial area is much wider and a median postaxial furrow is not developed. In addition, *P. ferox* has often a crescentic-shaped border between the pair of pygidial posterolateral spines. *P. fallax* in contrast, has a equally narrow border in between the spines developed (Høyberget and Bruton, 2008).

P. scutalis differs from *P. fallax* by narrow border furrows of cephalon and pygidium. The pygidium shows more distinguishing characters like a subcircular to semiovate form. The axis is lanceolate with a smaller axial node and a secondary median node on the midpoint of the posteroaxis. A median postaxial furrow is developed and the pygidium is spineless.

Brøgger (1879) pictured two complete specimens. Fig. 1 shows all characterestics of this species while the pygidium in fig. 1 a additionally has a third spine at the pygidial margin, in the middle of the pair of posterolateral spines. Because of this feature fig. 1 a is here not assigned to *P. fallax*. Linnarsson (1879) pictured a cephalon without the characteristic wide border furrow. The pygidium is absent, which shows the main distinguishing features for this species. Thus, an assignemt to *P. fallax* is doubtful.

Tullberg (1880) divided *P. fallax* in two subspecies: *Agnostus fallax typica* and *A. fallax ferox*. The subspecies *typica* is illustrated as a cephalon which agrees well with *P. fallax* but the axis of the pygidia is ogival and shows not the characteristic broad form. Therefore, the assignment of the pygidium to this species is questionable. Neverthless an intraspecific variation is possible.

Matthew (1886) figured *A. acadicus* the cephalon matches with *P. fallax*, but the pygidium in fig. 5 b is here assigned to *Hypagnostus parvifrons*. As discussed above, the figured pygidium shows the characteristic lanceolate axis, spineless and the distinct forward projection of the posterior border. Matthew (1886) described the new species *Agnostus vir* and the subspecies *A. vir concinnus*. Both illustrations show the cephalic and pygidial wide border furrows, broad pygidial axis with a large axial node and a pair of posterolateral spines. Matthew (1886) wrote, *A. vir* is distinguished from *P. fallax* by the form of the anterior glabellar lobe and the trisection segmentation of the posterior thorax segment. *A. vir concinnus* is closely related and with more narrow lateral furrows of the glabella. These described characters by Matthew (1886) are here suggested to be intraspecific variations and therefore assigned to be synonyms of *P. fallax*. Because of the above described variability within *P. fallax* it is here suggested to avoid the usage of subspecies, as also discussed by Robison (1982).

The pygidium of Matthew (1896, fig. 8 b) shows a wide border furrow, but the pygidial axis is very broad and too short, thus it is here assigned to *P. ferox*. Matthew (1896) illustrated *A. fallax concinnus* with the characteristic wide border furrow of the pygidium, but the cephalon has only a narrow border furrow. Posibly the cephalon shows a meraspis stage, therefore the assignment to *P. fallax* is considered questionable.

Lorenz (1906) described the new subspecies *Agnostus fallax laiwuensis*. The cephalon and pygidium show the wide border furrows, broad pygidial axis with a large axial node that reaches the border furrow and a pair of posterolateral spines. The subspecies is distinguished from *P. fallax* by the faint furrows at the posterior end of the posteroaxis. In addition, the described character by Lorenz (1906) is here suggested to be an intraspecific variation of *P. fallax*.

Grabau and Shimer (1910) figured a cephalon and pygidium of *A. acadicus*. The pygidium is here not assigned to *P. fallax* because the pair of posterolateral spines is absent and the pygidial axis is too broad. Howell (1925) described the new species *Agnostus clarae* by pygidia. The figured pygidium is subquadrate, has a wide border furrow, a long axis and a apir of posterolateral spines. Howell (1925) described the species with a short axis and mentioned a conection to *P. fallax* and *P. ferox*. Because of the typical characterostics the species is here assigned to *P. fallax*.

Strand (1929) described and figured two different species. He characterized the wide border furrows, the pygidial pair of posterolateral spines and the long axis. Illustrated are cephala and pygidia from *Hypagnostus parvifrons*, with the effaced anterior glabellar lobe which is half half as long as the cephalon and the nonspinose pygidia show the distinct forward projection of the posterior border (see Chapter *Hypagnostus parvifrons*). It is here suggested that Strand (1929) figured the wrong species, so it is here not assigend to *P. fallax*.

The illustrated specimens of Hutchinson (1952) and Henningsmoen (1952) are poorly preserved, there are no characteristics visible. Therefore any assignment is questionable. Dean (1982) illustrated four cephala and two pygidia of *P. fallax minor*, which all show the typical charcaters of *P. fallax* such as a wide border furrow, the elongate pygidial axial node and the pair of posterolateral spines. Egorova *et al.* (1982) figured several cephala and pygidia of *P. fallax*. A cephalon and two pygidia a poorly preseved, so any assignment is here suggested to be questionable. Samson *et al.* (1990) figured a cephalon and a pygidium of *P. fallax*. Fig. 5 B is here not assigned to the species, because the pair of pygidial posterolateral spines is absent. Weidner and Nielsen (2009) illustrated a cephalon and pygidium, which are poorly perserved, so an assignment is here considered to be doubtful.

Occurrence. *Peronopsis fallax* is a common, widespread and long ranging species in the middle Cambrian (gobal *Ptychagnostus gibbus* Zone to the upper *Ptychagnostus atavus* Zone) of southeastern Canada (Newfoundland, western Newfoundland, New Brunswick, Nova Scotia), USA (Nevada, Utah and South Carolina), Greenland, Sweden, Norway, Denmark, England, Spain, Germany (in erratic boulders), Turkey, Siberia, Australia and Antarctica.

Peronopsis scutalis (Hicks, 1872)
(Text-figs. 17 A–B)

1872 *Agnostus scutalis*, Salter *in* Hicks, p. 175, pl. 5, figs. 12–14.
1880 *Agnostus parvifrons* Linrs. Forma 1.; Tullberg, pp. 34–35, pl. 2, fig. 26.
1902 *Agnostus exaratus* n. sp. Grönwall, p. 77, pl. 1, fig. 17.
1906 *Agnostus exaratus*, Grönwall; Lake, pp. 6–8, pl. 1, figs. 8–10.
1915 *Agnostus exaratus* Grönwall; Illing, p. 405, pl. 28, fig. 1.
1915 *Agnostus exaratus* Grönwall, var. *tenuis* nov. Illing, p. 406, pl. 28, figs. 2–5.
pars 1946 *Peronopsis scutalis* (Salter in Hicks, 1872); Westergård, pp. 41–42, pl. 4, figs. 4–8 (not 9–11).
1962 *Peronopsis (Acadagnostus) scutalis* (Salter in Hicks); Hutchinson pp. 72–73, pl. 6, figs. 1–5.
1969 *Peronopsis scutalis* (Salter in Hicks, 1872); Poulsen, pp. 6–7, figs. 6 A–B.
1979 *'Acadagnostus scutalis'* (Salter, 1872); Öpik, pp. 63–64, pl. 2, fig. 5; Text-fig. 17.
? 1979 *Peronopsis scutalis scutalis* (Hicks 1872); Rushton, p. 50, fig. 5 C.
1979 *Peronopsis scutalis tenuis* (Illing 1915); Rushton, pp. 50–51, fig. 3 G.
non 1982 *Peronopsis scutalis* (Salter in Hicks, 1872); Egorova *et al.*, p. 67, pl. 58, figs. 1–2.
1988 *Peronopsis scutalis* (Hicks, 1872) *exarata* (Grönwall, 1902); Martin and Dean, pp. 16–17, pl. 4, figs. 3, 8.
1994 *Peronopsis scutalis* (Hicks, 1872); Robison, pp. 46–47, figs. 21.1–9.
1994 *Acadagnostus scutalis* (Salter in Hicks); Rudolph, p. 154, pl. 10, figs. 12–13.

1994 *Acadagnostus exaratus* (Grönwall 1902); Rudolph, pp. 154–155, pl. 10, figs. 14–15.

? 1996 *Peronopsis* cf. *P. scutalis* (Hicks, 1872); Westrop *et al.*, p. 822, figs. 22.7, 22.9–12.

2006 *Peronopsis scutalis* (Salter in Hicks, 1872); Fletcher, pp. 66–67, pl. 34, fig. 55.

2008 *Peronopsis scutalis* (Hicks 1872); Høyberget and Bruton, pp. 33–34, pl. 4, figs. A–C.

2014 *Acadagnostus scutalis* (Hicks, 1872) (*s.l.*); Weidner and Nielsen, pp. 40–41, figs. 33 A–D.

Diagnosis. Cephalon subcircular to subquadrate; glabella approximately two-thirds of cephalon length; long anterior glabellar lobe; small basal lobes; cephalon and pygidium nonspinose; border furrows narrow; pygidium subcircular to semiovate; pygidial axis lanceolate with well-tapered end, axial node on M2; small secondary median node at midpoint of posteroaxis; median postaxial furrow deep (based on Robison, 1994, with modifications).

Lectotype. Specimen no. SMA 1050, Sedgwick Museum, University of Cambridge, UK, by subsequent designation of Rushton (1979); originally figured by Hicks (1872, pl. 5, fig. 12) and refigured by Lake (1906, pl. 1, fig. 8).

Material. 25 cephala and 26 pygidia (NFM F-1275–F-1325) from the lowermost third part of the Manuels River Formation (1.95–7.13 m), type locality, Conception Bay South, Newfoundland, Canada. Most specimens were collected from the interval 1.95–2.13 m, in the upper part specimens of *P. scutalis* occur rarely.

Description. The specimens are mainly well preserved. The size of the cephala varies from 1.3 to 3.4 mm in width and from 1.2 to 3.4 mm in length. The size of the pygidia varies from 2.5 to 4.6 mm in width and from 2.4 to 4.8 mm in length. At the 2.55 m level two pygidia collected show a yellow surface from the pyrite contained in the shale.

All cephala and pygidia show the characteristic subcircular to subquadrate shape. Anteriorly the specimens have a broadly rounded anterior glabellar lobe and posteriorly a straight F3 furrow. There is a larg variation in the pygidia. The width of the pygidial border is in some specimens narrow in others wider. In some specimens the small, secondary median node is visible, situated at the midpoint of the lanceolate posteraxis, problably a matter of preservation. The pygidial pleural fields are rounded anteriorly and separated by a deep,

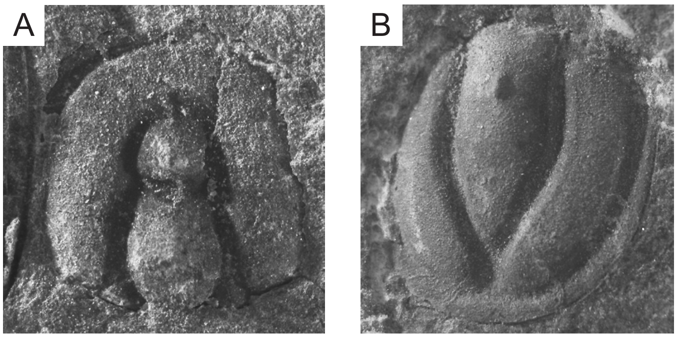


Fig. 17: *Peronopsis scutalis* (Hicks, 1872); **A**, cephalon (NFM F-1275), ×15; **B**, pygidium (NFM F-1276), ×15.

median, postaxial furrow. The length of the postaxial furrow varies in some specimens.

Discussion. *Peronopsis scutalis* shows morphological variations within populations (Robison, 1994; Høyberget and Bruton, 2008; Weidner and Nielsen, 2014). The cephalon changes less than the pygidia troughout ontogeny and within populations. The cephala show a small axial node on the posterior glabellar lobe. In some specimens, the node is not visible, which is probably a matter of preservation. Westergård (1946) described cephala and pygidia from Sweden with a length of 2–3 mm. Larger cephala and pygidia are rare. By contrast, 5–6 mm long cephala and pygidia from Greenland are common (Robison, 1994). In the present study, the length of the cephala and pygidia match well with the Swedish specimens described by Westergård (1946).

The pygidia varies in length and width of the axis (Westergård, 1946; Weidner and Nielsen, 2014). The length of the axis extends to two-thirds of the pygidial length with, in some specimens, a posteriorly tapered end. Usually, the pygidial pleural fields have nearly the same width as the axis and the ends are rounded to straight, the axis becomes longer and axial and border furrows deeper througout ontogeny and in larger specimens (Robison, 1994). The pleural fields are separated by a deep, median postaxial furrow. The small secondary median node at midpoint of the posteroaxis varies from weak to absent, which is probably a matter of preservation (Weidner and Nielsen, 2014).

P. scutalis is distinguished from other species of *Peronopsis* by the long anterior glabellar lobe, the small basal lobes, the very narrow border furrows and the absence of spines (Høyberget and Bruton, 2008).

Hicks (1872) listed in his description of *P. scutalis* Salter (1866), who first mentioned the species name in his report. Therefore, especially in older studies Salter (1866) is listed in several synonymy lists (in e.g. Lake, 1906). Salter (1866) mentioned the name *P. scutalis* without a description of the species, thus he compiled a "nomen nudum". According to the International Rules of Zoological Nomenclature the name and date with the first description of a species is valid, thus Hicks (1872) is here listed.

Tullberg (1880, fig. 26) figured a pygidium of *Hypagnostus parvifrons*. The pygidium shows a long pygidial axis, tapered posteriorly and F1 and F2 furrows are absent. These characters are typical of *P. scutalis*. Grönwall (1902) described the species *Agnostus exaratus*, figuring a single pygidium, which shows a relatively broad and short pygidial axis, rounded pleural fields and a median postaxial furrow. The broader pygidial axis is an intraspecific variation and the other specific characters match with *P. scutalis*. Therefore the species *A. exaratus* is here assigned as a synonym. Illing (1915) described the subspecies *A. exaratus tenuis*, distinguished from *P. scutalis* by its larger size, the subquadrate shape of the anterior glabellar lobe and narrower and more tapering pygidial axis. The figured specimens show relatively short pygidial axis but agree well with *P. scutalis*. Illing's (1915) described and figured characters are here suggested intraspecific variations of *P. scutalis*.

The figured pygidia of Westergård (1946, figs. 9–11) show a broad axis, posteriorly rounded pleural fields and a forward-projection of the broad pygdidial border furrow. These specific characters are typical of *Hypagnostus parvifrons* and therefore here not assigned to *P. scutalis*. Hutchinson (1962) followed a concept with subgenus *P. (Acadagnostus) scutalis* but nevertheless his illustrated specimens match with *P. scutalis* and here are assigned to this species. Öpik (1979) and later Rudolph (1994) and Weidner and Nielsen (2014) assigned *scutalis* to the genus *Acadagnostus* Kobayashi, 1939. As discussed under the genus *Peronopsis* (see Chapter *Peronopsis*) this species is nonspinose, thus, it is here assigned to *Peronopsis*.

Rushton (1979) divided *P. scutalis* in the subspecies *P. scutalis scutalis* and *P. scutalis tenuis*.

He figured a pygidium of *P. scutalis scutalis*, which is poorly preserved and seems to be impressed at the posterior part. Therefore the assignment to *P. scutalis* is questionable. The figured complete specimen of *P. scutalis tenuis* shows the typical cephalon with the big anterior glabellar lobe and the cephalic small axial node. The pygidium has a short but well-tapered end, which is characteristic of *P. scutalis*. Thus the subspecies of Rushton (1979) is here considered a synonym of *P. scutalis*.

Egorova *et al.* (1982) illustrated two specimens of *P. scutalis*. The cephalon is semiovate, the anterior glabellar lobe small and subcircular and the posterior glabellar lobe long. The pygidium shows a long and broad axis. Both figured specimens have broad border furrows and axial furrows. These characters are not specific of *P. scutalis*. Martin and Dean (1988) described the subspecies *P. scutalis exarata*. The figured cephalon and pygidium show all specific characters of *P. scutalis* and so it is here assigned to this species. Westrop *et al.* (1996) figured a cephalon and three pygidia of *P. scutalis*. All pygidia are poorly preserved, because the axis are fragmentary. Westrop *et al.* (1996) remarked that their few specimens are not enough for a confident identification, therefore the assignement to *P. scutalis* is doubtful.

Høyberget and Bruton (2008) erroneously listed "Dean 1982" for Martin and Dean (1988) in their synonymy list.

As discussed above, *P. scutalis* is a highly variable species and the attempts by many authors to split this species into subspecies was common in the past and here considered unjustified. Thus, the broad species concept of Westergård (1946), Rushton (1979), Robison (1994), Westrop *et al.* (1996), Høyberget and Bruton (2008) and Weidner and Nielsen (2014), is followed here.

Occurrence. *Peronopsis scutalis* is a common and widespread species in the middle Cambrian (global *Ptychagnostus gibbus* Zone to the *Lejopyge laevigata* Zone) of southeast Canada (Newfoundland), Greenland, Wales, England, Sweden, Norway, Denmark, Germany (in erratic boulders) and Australia.

Genus *Hypagnostus* Jaekel, 1909

Type species. *Agnostus parvifrons* Linnarsson, 1869, by original designation.

Diagnosis. Cephalon with effaced anterior glabellar lobe; F3 furrow rounded or truncated; median preglabellar furrow absent; posterior glabellar lobe short with glabellar node; pygidial border broader than the cephalic border; pygidial axis long (based on Robison, 1964; Westrop *et al.*, 1996; Whittington *et al.*, 1997, with modifications).

Synonyms. *Spinagnostus* Howell, 1935; *Cyclopagnostus* Howell, 1937.

Remarks. The most conspicuous character of *Hypagnostus* Jaekel, 1909, are the effacement of the anterior glabellar lobe, the short posterior glabellar lobe and the absence of a median preglabellar furrow (Westergård, 1946; Peng and Robison, 2000). Intraspecific variations in large populations are pygidial specific characters such as faint to absent F1 and F2 furrows on the axis, various combinations of shape and length of the axis, a weak axial node, a median postaxial furrow and a pygidial pair of posterolateral spines may be present (Peng and Robison, 2000). Because of these variable characters, the systematic position and the assignment of synonyms of *Hypagnostus* are still controversial discussed.

Shergold *et al.* (1990) and Whittington *et al.* (1997) assigned *Hypagnostus* to the Subfamily Spinagnostinae Howell, 1935. Westrop *et al.* (1996) followed the concept of Robison

(1994) to leave *Hypagnostus* in the Family Peronopsidae, because of the uncertainty about the monophyly of Spinagnostinae. Both, Spinagnostinae and Peronopsidae, are pimarly determined by the effacement of the anterior glabellar lobe, which might be polyphyletic.

Westrop *et al.* (1996) considered *Cotalagnostus* a synonym of *Hypagnostus*. Here, the concept of Peng and Robison (2000) is followed, who consider *Cotalagnostus* a separate genus. *Cotalagnostus* is distinghuised from *Hypagnostus* by an absent glabellar F3 furrow and faint to absent pygidial furrows surrounding the posteroaxis (Whittington *et al.*, 1997).

In the past, *Tomagnostella* was considered a synonym of *Hypagnostus* (e.g. Westergård, 1946; Robison, 1964). Here, the concept of Westrop *et al.* (1996) is followed, who treated both as separate genera on the basis of pygidial axis character such as distinct F1 and F2 furrows.

Hypagnostus parvifrons (Linnarsson, 1869)
(Text-figs. 18 A–C)

1869 *Agnostus parvifrons* n. sp. Linnarsson, p. 82, pl. 2, figs. 56–57.
pars 1880 *Agnostus parvifrons* Linrs.; Tullberg, pp. 34–35, pl. 2, figs. 27–28 (not 26).
pars 1886 *Agnostus acadicus*, Hartt; Matthew, p. 70, pl. 7, fig. 5 b (not 5 a).
pars 1886 *Agnostus acadicus*, var. *declivis*, n. var. Matthew, pp. 70–71, pl. 7, fig. 6 b (not 6 a).
1886 *Agnostus umbo*, n. sp. Matthew, pp. 71–72, pl. 7, figs. 8 a–b.
pars 1896 *Agnostus acadicus* Hartt; Matthew, pp. 217–219, pl. 15, fig. 10 b (not 10 a).
pars 1896 *Agnostus acadicus* Hartt var. *declivis* Matthew; Matthew, pp. 219–220, pl. 15, fig. 11 b (not 11 a, c–d).
1906 *Agnostus parvifrons*, Linnarsson, nov. var. *latelimbatus* Lorenz, p. 84, pl. 4, figs. 9 a–b; pl. 5, figs. 10–11.
1909 *Hypagnostus parvifrons* Linnars. sp.; Jaekel, pp. 398–399, fig. 17.
1913 *Agnostus parvifrons latelimbatus* Lorenz; Walcott, p. 102, pl. 7, figs. 1–1 a.
? 1915 *Agnostus parvifrons* Linnarsson; Illing, p. 422, pl. 32, fig. 10.
non 1925 *Agnostus parvifrons punctifer*, new variety Howell, pp. 78–80, pl. 3, figs. 4–5.
1929 *Agnostus parvifrons* Lnrs.; Strand, p. 347, pl. 1, fig. 14.

1929 *Agnostus fallax* Linrs.; Strand, p. 346–347, pl. 1, fig. 19.

non 1934 *Agnostus parvifrons*, Linnarsson; Cobbold and Pocock, pp. 343–344, pl. 44, figs. 13–19.

1939 *Hypagnostus parvifrons* Linnarsson, 1869; Kobayashi, pp. 122–128, fould-out chart in appendix.

1939 *Hypagnostus clipeus* sp. nov. Whitehouse, pp. 263–264, pl. 25, figs. 25–26.

1946 *Hypagnostus parvifrons* (Linnarsson, 1869); Westergård, p. 45, pl. 4, figs. 27–31.

1948 *Hypagnostus métisensis*, n. sp. Rasetti, pp. 320–321, pl. 45, figs. 21–27.

1959 *H. parvifrons* (Linnarsson); Harrington *et al.*, p. 185, figs. 126.1 a–b.

1962 *Hypagnostus parvifrons* (Linnarsson); Hutchinson, p. 73, pl. 6, figs. 6 a–b, 7.

1964 *Hypagnostus parvifrons* (Linnarsson); Robison, p. 529, pl. 81, figs. 4–23.

? 1967 *Hypagnostus parvifrons* (Linnarsson); Rasetti, pp. 34–35, pl. 9, figs. 23–25.

1979 *Hypagnostus clipeus* Whitehouse, 1939; Öpik, pp. 67–68, pl. 5, figs. 1, 7; text-fig. 18.

1979 *Hypagnostus parvifrons* (Linnarsson, 1869); Öpik, pp. 66–67, pl. 6, figs. 7–8.

? 1982 *Hypagnostus parvifrons* (Linnarsson, 1869); Egorova *et al.*, p. 69, pl. 9, fig. 1; pl. 12, fig. 11; pl. 17, fig. 8; pl. 40, fig. 3.

1984 *Hypagnostus parvifrons* (Linnarsson); Palmer *et al.*, p. 93, figs. 2 G–H.

? 1990 *Hypagnostus parvifrons* (Linnarsson, 1869); Samson *et al.*, p. 1466, figs. 5 H–J.

1990 *Hypagnostus parvifrons* (Linnarsson, 1869); Shergold *et al.*, pp. 80–81, figs. 13.1 a–b.

non 1992 *Hypagnostus* cf. *parvifrons* (Linnarsson, 1869); Fatka and Kordule, pl. 2, fig. 1.

1994 *Hypagnostus parvifrons* (Linnarsson, 1869); Robison, p. 41, fig. 17.1–2.

non 1994 *Hypagnostus parvifrons parvifrons* (Linnarsson 1869); Rudolph, pp. 130–131, pl. 7, figs. 6–11.

1995 *Hypagnostus parvifrons* (Linnarsson); Robison, p. 303, figs. 1.4–6.

1996 *Hypagnostus parvifrons* (Linnarsson, 1869); Westrop *et al.*, pp. 823–824, figs. 23.1–11.

1997 *Hypagnostus parvifrons* (Linnarsson, 1869); Tortello and Bordonaro, pp. 78–79, figs. 3.20–22.

- 1997 *H. parvifrons* (Linnarsson); Whittington *et al.*, p. 357, figs. 226.5 a–b.
- 2000 *Hypagnostus parvifrons* (Linnarsson, 1869); Peng and Robison, pp. 60–63, figs. 45.1–11.
- 2003 *Hypagnostus parvifrons* (Linnarsson, 1869); Axheimer and Ahlberg, p. 144, figs. 4 F–G.
- 2006 *Hypagnostus parvifrons* (Linnarsson, 1869); Fletcher, pp. 66–67, pl. 34, figs. 49–50.
- 2008 *Hypagnostus parvifrons* (Linnarsson 1869); Høyberget and Bruton, pp. 36–37, pl. 4, figs. D–L.
- *non* 2009 *Hypagnostus parvifrons* (Linnarsson, 1869); Fatka *et al.*, p. 123, figs. 2 C–D.
- 2009 *Hypagnostus parvifrons* (Linnarsson, 1869); Weidner and Nielsen, pp. 264–265, figs. 14 A–B, D–E.
- 2014 *Hypagnostus parvifrons* (Linnarsson, 1869); Weidner and Nielsen, pp. 26–27, figs. 21 C–D, 22 P.

Diagnosis. Short oval posterior glabellar lobe not exceeding half the length of cephalon; cephalon and pygidium nonspinose; pygidial axis with effaced F1 and F2 furrows; pygidial axial node weak, located at anterior part of axis; pleural fields divided by median postaxial furrow; pygidial border showing forward projection (based on Robison, 1964; Høyberget and Bruton, 2008, with modifications).

Lectotype and Paralectotype. Specimen no. SGU 4769 as lectotype (cephalon) and specimen no. SGU 4768 as paralectotype (pygidium), Geological Survey of Sweden, Uppsala, by subsequent designation of Westergård (1946, pl. 4, figs. 27–28), refigured by Whittington *et al.* (1997, figs. 226. 5 a–b). The cephalon and pygidium were illustrated originally by Linnarsson (1869, pl. 2, figs. 56–57).

Material. Two complete specimens, 23 cephala and 11 pygidia (NFM F-1326–F-1361) from the uppermost third part of the Manuels River Formation (11.20–16.17 m), type locality, Conception Bay South, Newfoundland, Canada. At level 2.75 m, specimens occur rare.

Description. The specimens are mainly poorly preserved. The two complete specimens are 4.9 mm and 6.6 mm long, respectively. The size of the cephala varies from 1.0 to 5.1 mm in width and from 1.1 to 4.8 mm in length. The size of the pygidia varies from 1.5 to 2.9 mm in width and from 1.7 to 2.8 mm in length. At the level of 12.62 to 12.65 m, the specimens

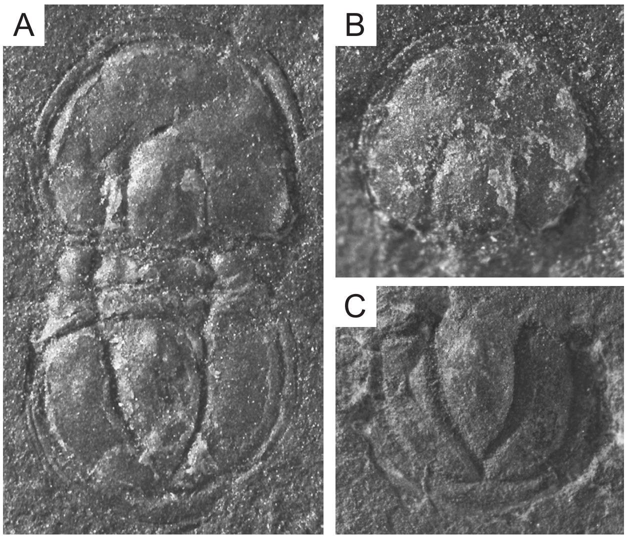


Fig. 18: *Hypagnostus parvifrons* (Linnarsson, 1869); **A**, complete specimens (NFM F-1326), ×10; **B**, cephalon (NFM F-1327), ×20; **C**, pygidium (NFM F-1328), ×15.

show a yellow surface, typical of the pyrite in the shales.

All cephala show the characteristic oval posterior glabellar lobe. In some cases the F3 furrow is truncated and vaguely defined. The small cephalic axial node is visible in several specimens; where absent, it is most likely a matter of preservation. In addition, some of the cephala show a weak scrobiculation on the cephalic genae. The cephalic border is narrow and the pygidial border broader. All the pygidia have a median postaxial furrow with posteriorly rounded pleural fields. The forward projection of the pygidial border is visible. The pygidial axis is in most of the specimens moderately broad and the axial node is always visible.

Discussion. *Hypagnostus parvifrons* shows several variable characters within populations (Westergård, 1946; Robison, 1964; Westrop *et al.*, 1996; Peng and Robison, 2000; Høyberget and Bruton, 2008). The cephala are variable in the length of the posterior glabellar lobe, which does not exceed half the length of the cephalon. Usually, the cephalic genae are smooth, but in some cases a weak scrobiculation is developed (Westergård, 1946; Peng and Robison, 2000; Høyberget and Bruton, 2008). The cephalic and pygidial width of the border is an intraspecific variation (Robison, 1964; Westrop *et al.*, 1996). The pygidial axis is long but variable in length and width (Peng and Robison, 2000). The pleural fields are always longer than the pygidial axis and in most cases rounded posteriorly. In addition, the length of the axis affects also the length of the median postaxial furrow.

The morphological changes during ontogeny of *H. parvifrons* are moderate, except for the increase in size. Specimens of an ontogenetic series were illustrated by Robison (1964).

H. parvifrons is distinguished from closely related species mainly by characteristics of the pygidia. As Weidner and Nielsen (2014) also described, there are no major differences between the cephala of *H. parvifrons* and *H. mammillatus*. *H. mammillatus* differs in having a broad pygidial border and the side view of the pygidium shows a high-piled axis. By contrast, the side view of *H. parvifrons* is slightly convex. Cephala of *H. frontosa* and *H. truncatus* show a longer glabella compared to that of *H. parvifrons*. *H. frontosa* differs from *H. parvifrons* in the lack of the forward projection of the pygidial border (Weidner and Nielsen, 2014). *H. truncatus* differs from *H. parvifrons* in having a wider cephalic border and a longer pygidial axis (Høyberget and Bruton, 2008).

As also discussed under *P. fallax* (Chapter *P. fallax*), Hartt in Dawson (1868) described the species *Agnostus acadicus*. This was later seen critical, because the sampled cephalon and pygidium of Dawson (1868) were not assigned to the equal species. Thus, Öpik (1979) and Robison (1995) proposed to assign the questionable type pygidium of Hartt to *Hypagnostus parvifrons* (Linnarsson, 1869). In the present study the suggestion of Høyberget and Bruton (2008) is followed, as shown under *P. fallax*.

Tullberg (1880) figured two complete specimens and a single pygidium. The pygidium shows a long, posteriorly tapered pygidial axis, where F1 and F2 furrows are absent. The pygidial pleural fields are not rounded as in *H. parvifrons* and there is no forward projection of the pygidial border visible. These characters agree with *P. scutalis*.

Matthew (1886) illustrated a cephalon and pygidium of *A. acadicus*. The pygidium shows the specific character of *H. parvifrons*. However, the figured cephalon is here not assigned to *H. parvifrons*, because of its subquadrate shape, wider border furrow and the presence of an anterior glabellar lobe. The specimens in fig. 5 a of Matthew (1886) is here assigned to *Peronopsis fallax* (see Chapter *P. fallax*). Matthew (1886) also described the new subspecies *A. acadicus declivis*. The figured pygidium of Matthew's (1886) fig. 5 b shows the same characters as *H. parvifrons*. The figured cephalon shows a shorter glabella than in fig. 5 a of Matthew (1886), but also an anterior glabellar lobe is visible. Therefore, it is here not assigned to *H. parvifrons*.

Furthermore, Matthew (1886) described the new species *Agnostus umbo*. The cephalon shows the typical oval posterior glabellar lobe, the effaced anterior glabellar lobe and the narrow border furrow. The figured pygidium shows the same character as described above for Matthew's (1886) figures 5 b and 6 b. *A. umbo* is here considered a synonym of *H. parvifrons*.

Matthew (1896) again illustrated the species *A. acadicus* and the subspecies *A. acadicus declivis*. The figured pygidia of *A. acadicus*, 10 b and the subspecies, fig. 11 b, are also here considered synonyms of *H. parvifrons*, because they show the typical characters as described above. Fig. 10 a matches well with the figured cephalon of Matthew (1886) and is therefore also assigned to *P. fallax*. The cephalon on fig 11 a of Matthew (1896) also shows the anterior glabellar lobe and is therefore not considered a synonym of *H. parvifrons*. One of the figured pygidia of *A. acadicus declivis*, fig. 11 c, shows faint horizontal furrows across the pygidial pleural fields and the anteroaxis. Another pygidium has five pits near the axial node on the axis. Because of these characters, the specimens shown in figs. 11 c–d are not assigned to *H. parvifrons*.

Lorenz (1906) described the new subspecies *Agnostus parvifrons latelimbatus*, which he distinguished from *H. parvifrons* by the broader pygidial posteriorly border. It is not as broad as in *H. mammillatus* and also the cephalon agrees closely with that of *H. parvifrons*. The figured pygidia show a relatively broad border, but fig. 9 b shows a side view of a flat specimens. This is typical of *H. parvifrons*, as shown by Høyberget and Bruton (2008), pl. 4, fig L. By contrast, the side view of *H. mammillatus* is high-piled. The characters described by Lorenz (1906) are here interpreted as intraspecific variations and therefore the separations as subspecies is unjustified.

Walcott (1913) figured a cephalon and a pygidium of the subspecies *A. parvifrons latelimbatus*. Both specimens show the characteristics of *H. parvifrons*.

The specimens figured by Illing (1915) are poorly preserved and a species assignment is here considered doubtful. The subspecies *A. parvifrons punctifer* described and figured by Howell (1925), shows a pygidium with a very broad border and a prominent axial node situated at the midpoint of the axis. The figure of a side view of the pygidium shows typical features of *H. mammillatus*.

Strand (1929) described *P. fallax*, but figured several species of *H. parvifrons*. Therefore, the figured specimens of *P. fallax* are here assigned to this species. Cobbold and Pocock (1934) figured pygidia with a broad border and a prominent axial node. These characters are typical of *H. mammillatus*.

Whitehouse (1939) described the new species *H. clipeus*, distinguished from *H. parvifrons* by the longer posterior glabellar lobe and the narrower border. But the figured specimens show the specific character of *H. parvifrons* and therefore *H. clipeus* is considered a synonym.

Rasetti (1948) described the new species *H. metisensis*. He noted, that this species is very close to *H. parvifrons*, from which it differs only by a narrower cephalic border. However, the figured specimens show all characters typical of *H. parvifrons*. In addition, it is here suggested that Rasetti's (1948) described variation of the cephalic border, is an intraspecific varition and therefore *H. métisensis* is here assigned a synonym of *H. parvifrons*, as also discussed by Robison (1964). Rasetti (1967) figured three cephala of *H. parvifrons* which show the oval posterior glabellar lobe half as long as the cephalon. Without a figured pygidium an assigment to *H. parvifrons* is questionable. Öpik (1979) figured one complete specimens and a pygidium of *H. clipeus* Whitehouse, 1939. The cephalon shows the specific characters and the pygidium has a shorter and more slender pygidial axis with a median postaxial furrow and posteriorly rounded pleural fields. The second pygidium shows a broad and longer axis with the posterior end near the border furrow. These characters are here suggested to be intraspecific variations of *H. parvifrons*.

All illustrated specimens of Egorova *et al.* (1982) and Samson *et al.* (1990) are poorly preserved and their assignments to *H. parvifrons* is here considered doubtful. Fatka and Kordule (1992) figured a complete specimen of *H.* cf. *parvifrons*, which is here assigned to *H. mammillatus*, because the pygidial border is too broad. For the same reason, Rudolph's (1994) figured specimens of *H. parvifrons parvifrons* are here assigned to *H. mammillatus*. As discussed above, Fatka *et al.* (2009) figured specimens which agree with those of Fatka and Kordule (1992) and are here assigned to *H. mammillatus*.

H. parvifrons was in the past an index fossil of the *H. parvifrons* Zone, which is not practicable because of the long stratigraphic range of the species (from the global lower *Ptychagnostus atavus* Zone to the *Ptychagnostus punctuosus* Zone) (Høyberget and Bruton, 2008).

Occurrence. *Hypagnostus parvifrons* is a widespread and long-ranging species in the middle Cambrian (global *Ptychagnostus atavus* Zone to the *Ptychagnostus punctuosus* Zone) of eastern Canada (Newfoundland, Québec, New Brunswick), USA (eastern Massachusetts, Utah, New York, Pennsylvania, South Carolina), Greenland, England, Sweden, Norway, Denmark, Germany (in erratic boulders), Siberia, China, Australia and Argentina.

Family Ptychagnostidae Kobayashi, 1939

Genus *Ptychagnostus* Jaekel, 1909

Type species. *Agnostus punctuosus* Angelin, 1851, by original designation (ICZN, 1993).

Diagnosis. Median preglabellar furrow; anterior glabellar lobe semiovate to ogival; posterior glabellar lobe with small axial glabellar node on M2 to rear part of M3; F1 and F2 of posteroglabella developed; basal lobes elongate, divided or entire; pygidial axis having F1 and F2 furrows of subequal depth and with node on M2; posteroaxis long, lanceolate to ogival; median postaxial furrow developed (based on Whittington *et al.*, 1997; Peng and Robison, 2000, with modifications).

Synonyms. *Triplagnostus* Howell, 1935; *Solenagnostus* Whitehouse, 1936; *Pentagnostus* Lermontova, 1940; *Huarpagnostus* Rusconi, 1950; *Canotagnostus* Rusconi, 1951; *Acidusus*

Öpik, 1979; *Aotagnostus* Öpik, 1979; *Aristarius* Öpik, 1979; *Zeteagnostus* Öpik, 1979.

Remarks. *Ptychagnostus punctuosus* (Angelin, 1851), the type species of *Ptychagnostus* (Jaekel, 1909), was originally described from an anthraconite boulder from Andrarum, Scania, Sweden. The generic characteristics of *Ptychagnostus,* such as spines, genal scrobiculation and surface granulation, are highly variable within populations (Robison, 1984; Peng and Robison, 2000; Ahlberg *et al.*, 2007).

Jaekel (1909) and Westergård (1946) included *Ptychagnostus* in the subfamily Agnostinae. Westergård (1946) divided the genus into two subgenera, *Ptychagnostus* and *Triplagnostus*.

The family Ptychagnostidae fulfills the requirements for good guide fossils in the Cambrian as discussed by Peng and Robison (2000), such as relatively short stratigraphic ranges, cosmopolitan distribution in open-marine facies and abundant occurrence.

Ptychagnostus punctuosus (Angelin, 1851)
(Text-figs. 19 A–C)

1851 *Agnostus punctuosus* Angelin, p. 8, pl. 6, fig. 11.
pars 1872 *Agnostus scutalis*, Salter; Hicks, p. 175, pl. 5, figs. 9–10 (not 11–14).
1875 *Agnostus punctuosus* Angelin, 1851; Brøgger, p. 576, pl. 25, fig. 2.
1879 *Agnostus punctuosus* Angelin, 1851; Brøgger, p. 67, pl. 6, figs. 12 a–b.
1880 *Agnostus punctuosus* Ang.; Tullberg, pp. 17–18, pl. 1, figs. 5 a–d.
1896 *Agnostus punctuosus* Angelin; Matthew, p. 232, pl. 16, figs. 11 a–b.
1906 *Agnostus punctuosus* Angelin; Lake, pp. 4–6, pl. 1, figs. 4–6.
? 1909 *Ptychagnostus punctuosus* Angelin; Jaekel, p. 400.
1915 *Agnostus punctuosus* Angelin; Illing, p. 409, pl. 29, figs. 2–3.
? 1925 *Agnostus punctuosus* Angelin; Howell, table 4.
1939 *Ptychagnostus punctuosus* Angelin, 1852; Kobayashi, pp. 152–153, fould-out chart in appendix.
1944 *Ptychagnostus punctuosus* (Angelin); Shimer and Shrock, p. 600, pl. 251,fig. 20.
1946 *Ptychagnostus (Ptychagnostus) punctuosus* (Angelin, 1851); Westergård, pp. 78–79, pl. 11, figs. 34–35; pl. 12, figs. 1–7.
v 1962 *Ptychagnostus punctuosus* (Angelin); Hutchinson, p. 84, pl. 9, fig. 16.
1962 *Ptychagnostus punctuosus* (Angelin); Hutchinson, p. 84, pl. 9, figs. 9–15,

17–19.

1967 *Ptychagnostus punctuosus* (Angelin); Rasetti, p. 28, pl. 9, figs. 28–30.

1969 *Ptychagnostus punctuosus* (Angelin, 1851); Poulsen, pp. 4–5, figs. 4 A–B.

1972 *Ptychagnostus (Ptychagnostus) punctuosus* (Angelin, 1851); Fletcher, pl. 5, figs. 1–2.

1979 *Ptychagnostus punctuosus fermexilis* subsp. nov. Öpik, p. 92, pl. 41, figs. 1–5.

1979 *Ptychagnostus punctuosus punctuosus* (Angelin, 1851); Öpik, pp. 89–91, pl. 38, fig 1; pl. 39, figs. 1–7, 9–10; pl. 40, fig. 1, text-fig. 26.

1980 *Ptychagnostus punctuosus* (Angelin, 1851); Ergaliev, pp. 70–71, pl. 1, fig. 25.

1981 *Ptychagnostus punctuosus* (Angelin); Allen *et al.*, pl. 16, fig. 1.

1982 *Ptychagnostus punctuosus* (Angelin, 1851); Egorova *et al.*, p. 64, pl. 11, figs. 4–5; pl. 12, figs. 5–6; pl. 13, figs. 9–12.

1984 *Ptychagnostus punctuosus punctuosus*; Berg-Madsen, figs. 4 D–G.

1984 *Ptychagnostus punctuosus* (Angelin); Robison, pp. 33–35, figs. 20.1–6b.

1985 *Ptychagnostus punctuosus fermexilis* Öpik; Xiang and Zhang, p. 73, pl. 21, figs. 9,12.

1985 *Ptychagnostus punctuosus punctuosus* (Angelin); Xiang and Zhang, pp. 73–74, pl. 20, figs. 4–5, 11, 15.

1988 *Ptychagnostus punctuosus* (Angelin 1851); Laurie, p. 172, fig. 1 A–F.

v 1988 *Ptychagnostus punctuosus* (Angelin, 1851); Martin and Dean, p. 17, pl. 4, figs. 5–6, 10.

1990 *Ptychagnostus punctuosus* (Angelin, 1851); Shergold *et al.*, figs. 11.1 a–b.

1994 *Ptychagnostus punctuosus* (Angelin 1851); Rudolph, pp. 108–110, pl. 4, figs. 1–12.

1997 *Ptychagnostus punctuosus* (Angelin); Whittington *et al.*, p. 351, figs. 223.1 a–b.

2000 *Ptychagnostus punctuosus* (Angelin, 1851); Peng and Robison, pp. 67–68, figs. 49.1–5.

2001 *Ptychagnostus punctuosus* (Angelin, 1851); Erlström *et al.*, p. 13, figs. 5 A–F.

2003 *Ptychagnostus punctuosus* (Angelin, 1851); Axheimer and Ahlberg, pp. 147–149, figs. 5 J–N, 6 A–E.

2003 *Ptychagnostus punctuosus* (Angelin); Peng, p. 139, figs. 2 D–E.

2004 *Ptychagnostus punctuosus* (Angelin, 1851); Weidner *et al.*, pp. 42–43, figs. 3 A–C.

2006 *Ptychagnostus punctuosus*; Axheimer, p. 15, figs. 6 E–F.

2006 *Ptychagnostus punctuosus* (Angelin, 1852 [sic]); Fletcher, pp. 66–67, pl. 34, figs. 53–54.

2008 *Ptychagnostus punctuosus* (Angelin 1851); Høyberget and Bruton, p. 49, pl. 8, figs. E–M.

2008 *Ptychagnostus punctuosus*; Laurie, pp. 212–213, pl. 1, fig. 8.

2009 *P. punctuosus*; Ahlberg *et al.*, p. 10, figs. 3 E–F.

Diagnosis. Cephalon subcircular to slightly subelliptical with narrow borders; genae strongly scrobiculate and granulose; posterior glabellar lobe trapezoid; cephalon and pygidium nonspinose; strong granules developed on pleural fields of pygidium; pygidial axis with F1 furrow bent strongly forward and F2 furrow bent backward, with elongate median axial node on M2; small secondary median node on posteroaxis faint to moderate developed (based on Öpik, 1979; Robison, 1984; John R. Laurie, 1988, with modifications).

Lectotype. Specimen no. Ar 9539, Swedish Museum of Natural History, Stockholm, Sweden, by subsequent designation of Westergård (1946, p. 78, pl. 12, figs. 3 a–b).

Material. Two complete specimens, 40 cephala and 41 pygidia (NFM F-1362–F-1444) from the upper part (16.72–19.00 m) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

Description. The specimens are mainly well preserved. The complete specimens are 9.0 mm and 11.1 mm long, respectively. The size of the cephala varies from 3.5 to 4.3 mm in width and from 3.6 to 4.4 mm in length. The size of the pygidia varies from 3.7 to 4.2 mm in width and from 3.5 to 4.3 in length.

All cephala and pygidia show the characteristic granulation. The median preglabellar furrow and the scrobiculate genae are visible. The anterior glabellar lobe is semiovate to triangular, in some specimens showing a sulcus, which extends the median preglabellar furrow. Probably this sulcus is either a matter of preservation or morphological intraspecific variation.

Discussion. *Ptychagnostus punctuosus* (Angelin, 1851) is a variable species, in different ontogenetic stages and also within populations (Illing, 1915; Westergård, 1946; Öpik, 1979; Robison, 1984). Holaspids differ from meraspids mainly in having a course genal surface granulation, prominent genal scrobicules and a longer and more defined pygidial axis. The

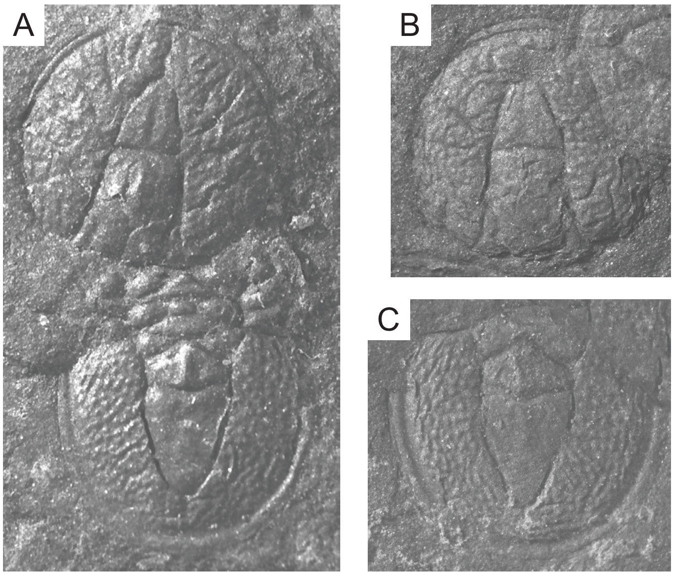


Fig. 19: *Ptychagnostus punctuosus* (Angelin, 1851); **A**, complete specimens (NFM F-1362), ×15; **B**, cephalon (NFM F-1363), ×15; **C**, pygidium (NFM F-1364), ×15.

median postaxial furrow is clearly developed in the meraspis stage and becomes fainter throughout ontogeny, as observed by Lake (1906) and Illing (1915). Axheimer and Ahlberg (2003) proposed five different ontogenetic stages of pygida of *P. punctuosus* on the data base of nine pygidia and four cephala. In this model he defined the change in the stages from meraspis to holaspis based on the previous mentioned characteristics. Although the definition is detailed, the low number of observed specimens is problematically for statistics.

In addition, variation of the diagnostic characters depend on the size of the specimens. Some larger specimens show a faint frontal sulcus on the anterior glabellar lobe which extends the median preglabellar furrow. The basal lobes vary from broad and triangular to elongate and entire or divided. The scrobiculate surface of the genae is very faint to strongly impressed and also the granulation of the genae and the pygidium varies from weak to strong. The median postaxial furrow is more developed in larger specimens, as also remarked by Westergård (1946).

Recognition of subgenera of *Ptychagnostus* and subspecies of *P. punctuosus* was common in the past (e.g., Westergård, 1946; Öpik, 1979; Berg-Madsen, 1984). The subspecies most frequently described are *P. punctuosus punctuosus* and *P. punctuosus affinis* (Brøgger, 1879).

Öpik (1979) introduced the subspecies *P. punctuosus fermexilis*. The typical characters are the slenderness of the glabella, the prominent node on M2 of the pygidial axis, the short median postaxial furrow and the absence of pygidial granulation on the pleural fields. These described characters may be variations within populations and ontogenetic stages of *P. punctuosus*. Also the pictures of the species match with *P. punctuosus*, therefore *P. punctuosus fermexilis* is here assigend to be a synonym of *P. punctuosus*.

Because of the wide morphological variability between ontogenetic stages and within populations it is here suggested to avoid the usage of subspecies, as also suggested by Robison (1984).

The closely related species *P. affinis* differs from *P. punctuosus* by the absence of genal granules and by the weakly developed pygidial granules on the pleural fields. *P. atavus* differs in in its absence of granules on the genae and the pygidial pleural fields.

Salter's (in Hicks, 1872) description of the species *Agnostus scutalis* and his two figs. 9–10, pl. 5, of pygidia match with *P. punctuosus*. The other figs. 11–14 show complete specimens of *Agnostus scutalis.* Howell (1925) reported the species from shales in the upper part of the type locality of Manuels River Formation (beds 95–120). The author agrees with Howell's occurrence of *P. punctuosus*. However, without proper description or illustrations the assignment must be considered tentative. The species was also mentioned by Jaekel (1909) but without descriptions or figures. He defined the genus *Ptychagnostus* by the species *P. punctuosus*.

Original specimens from Manuels River in the collections of Hutchinson (1962), GSC No. 13048 and Martin and Dean (1988), GSC Nos. 83300–83302, have been checked. However, the origin of the material remains uncertain, as also remarked by Austermann (2016). The lithology differs significantly from that of the specimens described in this study. Hutchinson's (1962) material appears to be loose samples from the east bank of the Manuels River as stated in his fieldbook. The origin of the material of Martin and Dean (1988) appears to be the same like Hutchinson's and is therefore also uncertain. In both studies (Hutchinson, 1962; Martin and Dean, 1988) are no detailed profiles, but they postulate that their specimens are from the west bank of the river. In comparison to the material studied here and the notes of the fieldbook from Hutchinson (1962), in either case happened a mislabelling, because the samples do not agree with those studied here from the west bank of the Manuels River.

Occurrence. *Ptychagnostus punctuosus* has a wide distribution in the middle Cambrian (global *Ptychagnostus punctuosus* Zone) of Canada (Newfoundland and New Brunswick), USA (New York, Nevada and Utah), England, Wales, Denmark, Norway, Sweden, Germany (in erratic boulders), Greenland, China and Australia.

Ptychagnostus affinis (Brøgger, 1879)

(Text-figs. 20 A–C)

1879 *Agnostus punctuosus*, Ang. var. *affinis* Brøgger, p. 68, pl. 5, figs. 2 a–b.

1946 *Ptychagnostus (Ptychagnostus) punctuosus affinis* (Brögger, 1878); Westergård, p. 79, pl. 11, figs. 26–33.

non 1968 *Ptychagnostus (Ptychagnostus) punctuosus affinis* (Brögger); Palmer, p. 28, pl. 4, figs. 26–27.

1979 *Ptychagnostus punctuosus affinis* (Brögger, 1878); Öpik, pp. 91–92, pl. 39, fig. 8; pl. 40, figs. 2–7.

1979 *Ptychagnostus mesostatus* sp. nov. Öpik, pp. 97–98, pl. 40, fig. 8; pl. 41, figs. 6–7.

1984 *Ptychagnostus affinis* (Brøgger); Robison, pp. 16–17, figs. 9.1–8.

1988 *Ptychagnostus affinis* (Brøgger 1878); Laurie, pp. 172–173, figs. 2 A–E.

1994 *Ptychagnostus affinis* (Brøgger, 1878); Robison, p. 55, figs. 10.5, 27.1–2.

? 1994 *Ptychagnostus affinis* (Brøgger 1878); Rudolph, pp. 110–111, pl. 4, figs. 15–16.

2000 *Ptychagnostus affinis* (Brøgger, 1878); Peng and Robison, pp. 68–69, fig. 51.

2003 *Ptychagnostus affinis* (Brögger, 1878); Axheimer und Ahlberg, p. 147, figs. 4 O–P, 5 A.

2007 *Ptychagnostus affinis*; Ahlberg *et al.*, p. 10, figs. 3 H–J.

2008 *Ptychagnostus affinis* (Brøgger 1878); Høyberget and Bruton, pp. 50–51, pl. 7, figs. N–X; pl. 8, figs. A–D.

2008 *Ptychagnostus affinis*; Laurie, pp. 212–213, pl. 1, fig. 9.

2009 *Ptychagnostus affinis* (Brøgger, 1878); Weidner and Nielsen, figs. 9 A–C, 10 C.

2010 *Ptychagnostus affinis* (Brøgger 1878); Jago and Bentley, p. 476, figs. 6 e–h.

2014 *Ptychagnostus affinis* (Brøgger, 1878); Weidner and Nielsen, pp. 14–15, figs. 13–14.

Diagnosis. Cephalic genae smooth; posterior glabellar lobe trapezoid; cephalon and pygidium nonspinose; weakly granulated pygidial pleural fields; M2 hexagonal in outline with elongate median axial node; small secondary median node on posteroaxis faint to moderate (based on

Robison, 1984; Laurie, 1988; Høyberget and Bruton, 2008, with modifications).

Lectotype. Specimen no. PMO 28148, Paleontologisk Museum University of Oslo, Norway, originally figured by Brøgger (1879, pl. 5, fig. 2a), refigured and designated as lectotype by Høyberget and Bruton (2008, pl. 7, fig. O).

Material. One complete specimen, 48 cephala and 50 pygidia (NFM F-1445–F-1543) from level 14.92–15.36 m of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

Description. The specimens are mainly well preserved. The complete specimen is 11.4 mm long. The size of the cephala varies from 2.7 to 5.2 mm in width and from 2.6 to 5.4 mm in length. The size of the pygidia varies from 3.1 to 4.7 mm in width and from 3.3 to 4.8 in length.

All cephala are scrobiculate with the median preglabellar furrow. Some specimens show a cephalic axial node is situated at the midpoint of the posterior glabellar lobe, others are absent. Possibly the absent node of some specimens is a matter of preservation. The pygidia show a long, lanceolate to moderately ogival axis with the characteristic hexagonal M2 in outline. The pygidial median axial node is elongate and the secondary median node, sometimes visible is situated at midpoint of the posteroaxis. The median postaxial furrow becomes fainter in larger specimens. The pygidial pleural fields are weakly granulated.

Discussion. This species is closely related to *Ptychagnostus atavus* (Tullberg, 1880), *Ptychagnostus punctuosus* (Angelin, 1851) and *Ptychagnostus intermedius* (Tullberg, 1880).

P. affinis differs from *P. atavus* by its weakly developed pygidial granules on the pleural fields compared to smooth pygidia by *P. atavus* (Westergård, 1946; Robison, 1984; Peng and Robison, 2000). The posteroaxis of *P. atavus* is more convex. *P. affinis* shows a lanceolate posteroaxis with 2–5 pairs of lateral impressions, on some swedish specimens (Weidner and Nielsen, 2009). Some specimens of *P. atavus* have a crescentic pair of furrows, located opposite the anterior glabellar lobe, which is an intraspecific variation. These furrows have not been described or pictured for *P. affinis*.

P. punctuosus is distinguished from *P. affinis* by strong granulation on cephala and pygidia (Westergård, 1946; Robison, 1984; Høyberget and Bruton, 2008). The axial node on the cephalon is more prominent and the pygidial posteroaxis is more rounded than in *P. affinis* (Høyberget and Bruton, 2008). These aspects show that *P. affinis* is an intermediate form between *P. atavus* and *P. punctuosus*, as discussed by several authors (Westergård, 1946; Robison, 1984; Peng and Robison, 2000; Axheimer and Ahlberg, 2003; Høyberget

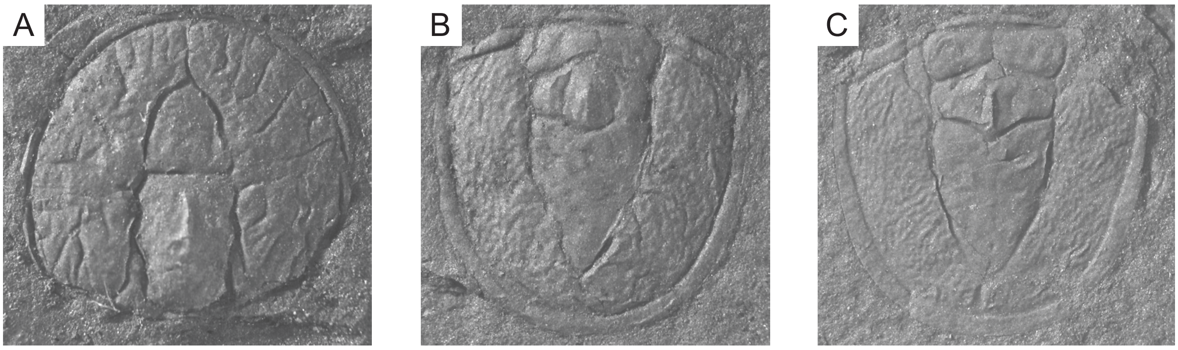


Fig. 20: *Ptychagnostus affinis* (Brøgger); **A**, cephalon (NFM F-1445), ×10; **B**, pygidium (NFM F-1446), ×10; **C**, pygidium (NFM F-1447), ×10.

and Bruton, 2008).

P. intermedius differs from *P. affinis* mainly in having a crescentic pair of furrows, located opposite the anterior glabellar lobe, a very faint and less elongate median axial node and a nearly straight F2 on the pygidium, which cause the typical pentagonal M2 in outline (Robison, 1984).

Brøgger (1879) described the subspecies *Agnostus punctuosus affinis* on the basis of only a few cephala. He postulated that these cephala, compared to *P. punctuosus*, have the same characters, only the pygidia show differences in granulation. *P. punctuosus* shows a strong granulation compared to *A. punctuosus affinis* with a fainter granulation on the pygidial pleural fields. The drawings of the subspecies agrees closely with *P. affinis*.

Between the description of *P. affinis* of Brøgger (1879) and the following of Westergård (1946) is a gap of 67 years. There are no other studies known of *P. affinis*. Recognition of subgenera of *Ptychagnostus* and subspecies of *P. punctuosus* was common in the past (Westergård, 1946; Palmer, 1968; Öpik, 1979). Figs. 26–27 of Palmer (1968) are here not assigned to *P. affinis* because the pygidial posteroaxis has a ogival form and there are no faint granules, which is not characteristic of *P. affinis*. The cephalon has a crescentic pair of furrows on the opposite side of the anterior glabellar lobe and a pair of pygidial posterolateral spines, characters that do occur in *P. affinis*.

Öpik (1979) introduced the new species *Ptychagnostus mesostatus* on the basis of one complete exoskeleton and one pygidium. The species was defined by the posterior glabellar lobe with paralell flanks. However, these characters are not visible in the illustrations. Therefore, the species must be considered questionable.

Robison (1984) elevated *P. punctuosus affinis* to species rank as *P. affinis*. Rudolph (1994) pictured two cephala, which are here considered questionable, because typical characteristics are not visible.

Occurrence. *Ptychagnostus affinis* has a wide distribution in the middle Cambrian (global the lower Ptychagnostus atavus Zone to the *Ptychagnostus punctuosus* Zone) and has been documented from southeastern Canada (Newfoundland), USA (Nevada and Utah), Denmark, Norway, Sweden, Germany (in erratic boulders), Greenland, China and Australia.

Ptychagnostus atavus (Tullberg, 1880)

(Text-figs. 21 A–C)

1880 *Agnostus atavus* n. sp. Tullberg, pp. 14–15, pl. 1, figs. 1 a–d.
non 1929 *Agnostus atavus* Tbg.; Strand, p. 344, pl. 1, fig. 20.
pars 1946 *Ptychagnostus (Ptychagnostus) atavus* (Tullberg, 1880); Westergård, pp. 76–77, pl. 11, figs. 8–18, 22–25 (not 19–21).
1962 *Ptychagnostus atavus* (Tullberg); Hutchinson, pp. 83–84, pl. 8, figs. 16–22; pl. 9, figs. 1–8.
1979 *Ptychagnostus atavus* (Tullberg, 1880); Öpik, pp. 93–94, pl. 29, fig. 7; pl. 42, figs. 7–8; pl. 43, figs. 1–4; text-fig. 27.
1979 *Ptychagnostus atavus coartatus* subsp. nov.; Öpik, pp. 94–95, pl. 42, figs. 5–6.
1979 *Ptychagnostus intermedius* (Tullberg, 1880); Öpik, p. 95, pl. 41, fig. 8.
1979 *Ptychagnostus (Acidusus) navus* sp. nov. Öpik, pp. 101–102, pl. 46, fig. 1.
1980 *Ptychagnostus atavus* (Tullberg, 1880); Ergaliev, pp. 67–69, pl. 1, figs. 13–17.
pars 1982 *Ptychagnostus atavus* (Tullberg, 1880); Egorova *et al.*, pp. 63–64, pl. 6, fig. 7; pl. 7, fig. 6.; pl. 11, figs. 1–3; pl. 13, fig. 13; pl. 55, figs. 16, 18, 20–21 (not pl. 51, fig. 11).
1982 *Ptychagnostus atavus* (Tullberg); Kindle, pl. 1.2, fig. 2.
1982 *Ptychagnostus atavus* (Tullberg); Robison, pp. 136–139, pl. 1, figs. 1–9.
1982 *Ptychagnostus atavus*; Rowell *et al.*, p. 165, text-fig. 5.
1984 *Ptychagnostus atavus* (Tullberg); Robison, pp. 18–21, figs. 11. 1–6.
1988 *Acidusus atavus* (Tullberg 1880); Laurie, p. 180, figs. 5 A–F.
1994 *Ptychagnostus atavus* (Tullberg, 1880); Robison, pp. 55–56, figs. 27.5–6.
? 1994 *Acidusus atavus* (Tullberg 1880); Rudolph, pp. 113–114, pl. 3, fig. 3.
1994 *Acidusus sterleyi* n. sp.; Rudolph, pp. 116–117, pl. 3, figs. 6–10.
1996 *Ptychagnostus* (s.l.) *atavus* (Tullberg, 1880); Westrop *et al.*, pp. 816–817, figs. 15.1–4.

2000 *Ptychagnostus atavus* (Tullberg); Pegel, p. 1013, fig. 11.13.

2000 *Ptychagnostus atavus* (Tullberg, 1880); Peng and Robison, pp. 69–70, figs. 52.1–8.

2003 *Ptychagnostus atavus* (Tullberg, 1880); Axheimer and Ahlberg, p. 147, figs. 5 B–C.

2006 *Ptychagnostus atavus*; Axheimer, figs. 6 G–H.

2006 *Acidusus atavus* (Tullberg, 1880); Fletcher, pl. 34, figs. 43–44.

2007 *Ptychagnostus atavus* (Tullberg, 1880); Ahlberg *et al.*, pp. 710–713, figs. 2.1–12.

2007 *Ptychagnostus atavus* (Tullberg); Babcock *et al.*, pp. 88–89, figs. 6 B–D, 7 B.

2008 *Ptychagnostus atavus* (Tullberg 1880); Høyberget and Bruton, pp. 49–50, pl. 7, figs. G–M.

2009 *Acidusus atavus* (Tullberg, 1880); Weidner and Nielsen, pp. 259–260, figs. 8 A–D, 10 A–B.

2014 *Acidusus atavus* (Tullberg, 1880); Weidner and Nielsen, pp. 10–13, figs. 9, 10 A–D, 11 A–H, 12 F–H.

2015 *Ptychagnostus atavus* (Tullberg, 1880); Hong and Choi, pp. 378–388, figs. 2. 1–8.

Diagnosis. Cephalon convex; posterior glabellar lobe trapezoid; cephalon and pygidium nonspinose; pygidial axis with hexagonal M2 in outline and prominent median node next to rear margin of M2; small secondary median node on posteroaxis faint to moderate (based on Robison, 1982; Robison, 1984; Peng and Robison, 2000, with modifications).

Lectotype. Specimen no. LO 354T, Department of Geology, Lund University, Sweden, by subsequent designation of Westergård (1946, p. 130, pl. 11, fig. 8), originally figured and designated as syntype by Tullberg (1880).

Material. Three complete specimens, 49 cephala and 55 pygidia (NFM F-1544–F-1650) from level 11.85–12.06 m of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

Description. The specimens are mainly well preserved. All complete specimens are preserved as moulds. The complete specimens are 3.7, 5.8 and 8.5 mm long, respectively. The size of the cephala varies from 3.4 to 5.0 mm in width and from 3.1 to 4.7 mm in length. The size

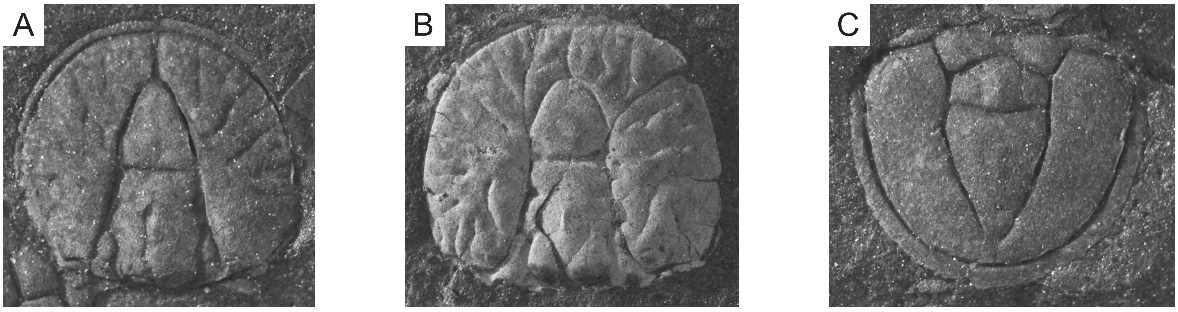


Fig. 21: *Ptychagnostus atavus* (Tullberg, 1880); **A**, cephalon (NFM F-1544), ×10; **B**, cephalon (NFM F-1545), ×10; **C**, pygidium (NFM F-1546), ×10.

of the pygidia varies from 2.2 to 4.1 mm in width and from 2.1 to 4.1 mm in length. Some of the specimens show a yellow surface, typically from the pyrite contained in the shales of the formation.

All specimens show the typical character such as scrobiculate genae, in larger specimens more prominently. All specimens show the median preglabellar furrow and the median postaxial furrow. The position of the nodes on the posterior glabellar lobe varies from the level where the basal lobes end (at the midpoint of M2) up to F2 furrow. Several specimens have no F2 furrows and the midpoint of the posterior glabellar lobe is similar to the level where the basal lobes end. The variations in the position of the glabellar node and the occurrence of the F2 furrow are probably due to intraspecific variation. The basal lobes are mostly elongate and entire.

Most of the pygidia show a long, moderately ogival axis, tapering to the median postaxial furrow. The characters such as hexagonal M2 in outline and the prominent median axial node are visible. The small secondary median node, is located at the midpoint of the posteraxis.

Discussion. *Ptychagnostus atavus* (Tullberg, 1880) is a common ptychagnostid species. It shows many morphological variations in different ontogenetic stages and also within populations (e.g. Westergård, 1946; Hutchinson, 1962; Robison, 1982; Peng and Robison, 2000; Ahlberg *et al.*, 2007; Weidner and Nielsen, 2014). The cephalon changes less than the pygidia throughout ontogeny. The meraspis stage is characterised by smooth to weak scrobiculate genae which grow stronger in the holaspis stage. Also, the median preglabellar furrow, as the median postaxial furrow, is clearly developed in the meraspis stage and becomes fainter throughout ontogeny (Westergård, 1946; Robison, 1982). The pygidial axis grow from a short and lanceolate to a longer and more ogival shape (Fig. 21 C). The F2 furrow is not yet developed in the meraspis stage and the axial node is often fainter than in the holaspis stage.

The diagnostic characters also vary within populations. Some cephali have a crescentic pair of furrows which may vary in size and shape. These furrows are located opposite the anterior glabellar lobe (Robison, 1982). None of the specimens in this study show these furrows as opposed to specimens for example, from Sweden (Westergård, 1946), western North America (Robison, 1982), western Newfoundland (Westrop *et al.*, 1996), Hunan in China (Peng and Robison, 2000) and Bornholm, Denmark (Weidner and Nielsen, 2014).

There is also considerable variation in the position of the axial node on the cephalon. The node is found on the middle of the posterior glabellar lobe and the horizontal level on M2 varies from the F1 to the F2 furrows (e.g. Westrop *et al.*, 1996; Ahlberg *et al.*, 2007; Weidner and Nielsen, 2009).

Other intraspecific variations are the two nodes on the pygidia and the shape of the axis. The median axial node is commonly prominent on the hexagonal M2 near the rear margin. The reason for this shape with the sometimes strongly backward-bent F2 furrow is the varying position of the node and also its size. Where the node is situated in the middle of M2, the F2 furrow is not as rounded as if the node is located near the margin of M2. The secondary median node is normally small and its position varies on the middle axis of the posteroaxis. It is often a matter of preservation if the node is strong, faint or absent. The shape of the posteroaxis varies from moderately ogival with a tapering axis to ogival and well rounded without a tip.

On account of these variations, the systematic position of *P. atavus* is controversial, as discussed by many authors (Westergård, 1946; Öpik, 1979; Robison, 1982; Robison, 1984; Laurie, 1988; Ahlberg *et al.*, 2007; Weidner and Nielsen, 2014). Jaekel (1909) erected *Ptychagnostus* and assigned *P. atavus* to this genus. Later, Westergård (1946) errected the subgenus *Ptychagnostus (Ptychagnostus)* and Öpik (1979) the subgenus *Ptychagnostus (Acidusus)*, with the main distinguishing character the presence of a pygidial terminal node. Laurie (1988) elevated *Acidusus* to genus rank. The main distinguishing characters stated by him are the position of the cephalic axial node next to F1 and a large pygidial axial node next to the F2 furrow. Laurie (1988) did not mention the pygidial terminal node like noted by Öpik (1979). Laurie (1988) assigned the species *atavus* to *Acidusus* but though he mentioned that *atavus* is not a typical representative of *Acidusus* because of the sometimes developed crescentic pair of furrows on the cephalic genae. Rudolph (1994), Fletcher (2006) and Weidner and Nielsen (2009; 2014) also assigned *atavus Acidusus*.

By contrast, it is here suggested to assign *atavus* to *Ptychagnostus*. *Acidusus* is considered to be a synonym of *Ptychagnostus* because of the variable morphological characters described above. Westergård (1946) and Robison (1994) postulate that the species *P. atavus*, *P. affinis* and *P. punctuosus* from a continuous evolutionary series.

The closely related species *P. affinis* differs from *P. atavus* by its weakly developed pygidial granules on the pleural fields. Isolated cephala of these species, therefore, may be difficult to distinguish. *P. punctuosus* differs by the strong granulation on the cephalic genae and the pygidial pleural fields. *P. intermedius* differs in having a weak pygidial median axial node, a pentagonal M2 in outline, faint granules on the pygidial pleural fields and an axial node on the cephalon generally located at the posterior glabellar midpoint, as discussed by Robison (1982).

The cephalon figured by Strand (1929) is here not assigned to *P. atavus* because the posterior glabellar lobe is too rounded and untypical of *P. atavus*. Westergård's (1946, figs. 19–21) specimens are assigned to *P. intermedius* on account of the characteristic pygidial pentagonal M2 (fig. 21). All figured specimens are syntypes, collected by Tullberg (1880).

Öpik (1979) described the new species *Ptychagnostus (Acidusus) navus* on the basis of a single complete specimen, which is here considered questionable. The distinguishing character to *P. atavus* is the absence of the median postaxial furrow, which, as discussed above, is possibly related to ontogeny or variations within population. *P. atavus coartatus* was described by Öpik (1979) on the basis of only two cephala. The cephala show the same characteristics as *P. atavus*. Therefore, the two new species of Öpik (1979) are considered synonyms of *P. atavus*. Furthermore, Öpik (1979) assigned a complete specimen to *P. intermedius* (Tullberg, 1880). Because the pygidium shows the characteristical hexagonal M2 in outline with a prominent median node, the specimen is better reffered to *P. atavus*.

Egorova *et al.* (1982, pl. 51) figured a cephalon. The cephalon is more subquadrate, i.e., not rounded and the characteristic scrobiculation of *P. atavus* is not seen in the figure.

Rudolph's (1994) single, figured pygidium of *Acidusus atavus* is poorly preserved and so any assignment is questionable. He also described the new species *A. sterleyi*, which he distinguished from *P. atavus* by the lanceolate shape of the pygidial axis and the shaped pygidial F2 furrow by the median pygidial node. These characters are intraspecific variations as described above and, therefore, these specimens are here assigned to *P. atavus*.

Occurrence. *Ptychagnostus atavus* is a common and widespread species in the middle Cambrian (global lower part of the *Ptychagnostus atavus* Zone to the lower part of the *Ptychagnostus punctuosus* Zone) of southeastern Canada (Newfoundland), USA (Utah and Nevada), Sweden, Denmark, Norway, Germany (in erratic boulders), Siberia, Kazakhstan, China, Korea, Australia and Greenland.

Genus *Tomagnostus* Howell, 1935

Type species. *Agnostus fissus* Lundgren in Linnarsson, 1879, by original designation.

Diagnosis. Genae scrobiculate; median preglabellar furrow weakly developed; anterior glabellar lobe subquadrate to semiovate; posterior glabellar lobe with well-developed F2 furrows and elongate axial glabellar node; basal lobes simple to slightly elongate; pygidial axis with well-developed F2 furrows; moderate to small axial node on M2; posteroaxis with transverse depression near midlength; median postaxial furrow weakly developed (based on Robison, 1994; Whittington *et al.*, 1997, with modifications).

Remarks. *Tomagnostus fissus* (Lundgren in Linnarsson, 1879), the type species of *Tomagnostus* (Howell, 1935), was originally described from the Exsulans Limestone Bed of Brantevik, Scania, Sweden. The systematic position of *Tomagnostus* is still under discussion. The genus has been assigned to the families Agnostidae, Diplagnostidae, Peronopsidae and Ptychagnostidae (Rushton, 1979; Shergold *et al.*, 1990; Robison, 1994).

According to Jaekel (1909) *Tomagnostus* is related to the Family Agnostidae. Howell (1935) defined the genus but did not assign it to a family. Together with the genus *Diplagnostus* Harrington (1938) placed *Tomagnostus* in the Peronopsidae. Kobayashi (1939) assigned *Tomagnostus* to the new subfamily Tomagnostinae in the family Agnostidae. Whitehouse (1936) and Westergård (1946) placed *Tomagnostus* in the Diplagnostidae. Later, Rushton (1979) suggested, that *Tomagnostus* resembles *Ptychagnostus* and therefore assigned them to the Agnostidae. Shergold *et al.* (1990) was the first to include *Tomagnostus* in the Family Ptychagnostidae.

According to Robison (1994), the widespread distribution of *Tomagnostus* suggests that these forms may have been adapted to cool-water regions with the range from shallow to deep water.

Tomagnostus fissus (Lundgren *in* Linnarsson, 1879)
(Text-figs. 22 A–C)

1879 *Agnostus fissus* Lundgren mscr. *in* Linnarsson, p. 23, pl. 2, fig. 34.
1880 *Agnostus fissus* Lundgr. mscr.; Tullberg, p. 16, pl. 1, figs. 3 a–d.

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

1906 *Agnostus fissus*, Lundgren MS.; Lake, pp. 3–4, pl. 1, figs. 1–3.

1915 *Agnostus fissus* Lundgren MS.; Illing, pp. 406–407, pl. 28, figs. 6–8.

1935 *Tomagnostus fissus* (Lundgren, M.S.); Howell, p. 15–16, figs. 9–10.

1946 *Tomagnostus fissus* (Lundgren MS; Linnarsson, 1879); Westergård, pp. 58–59, pl. 7, figs. 21–29; pl. 16, fig. 8.

1959 *Tomagnostus fissus* (Lundgren); Harrington *et al.*, p. 175, fig. 114.4.

1962 *Tomagnostus fissus* (Lundgren MS; Linnarsson); Hutchinson, pp. 76–77, pl. 7, figs. 1–5.

1982 *Tomagnostus fissus* (Lundgren in linnarsson, 1879); Egorova *et al.*, p. 59, pl. 3, figs. 1–4b; pl. 4., fig. 1; pl. 6, fig. 6; pl. 8, figs. 4–7; pl. 9, fig. 5; pl. 51, figs. 7–8.

1982 *Tomagnostus fissus* (Lundgren ms, Linnarsson); Kindle, pp. 4–5, pl. 1.2, figs. 6, 10.

? 1990 *Tomagnostus fissus* (Linnarsson, 1879); Samson *et al.*, p. 1467, figs. 5 C–E.

1990 *Tomagnostus fissus* (Lundgren in Linnarsson, 1879); Shergold *et al.*, p. 41, figs. 12.6 a–b.

1994 *Tomagnostus fissus* (Linnarsson, 1879); Robison, pp. 59–60, figs. 30.1–10.

1994 *Tomagnostus fissus* (Lundgren in Linnarsson 1879); Rudolph, pp. 127–128, pl. 8 figs. 11–13.

1996 *Ptychagnostus (Ptychagnostus) fissus* (Lundgren, in Linnarsson, 1879); Westrop *et al.*, pp. 819–820, figs. 18.1–7.

1997 *Tomagnostus fissus* (Lundgren); Whittington *et al.*, p. 354, figs. 224.3 a–b.

2000 *Tomagnostus fissus* (Lundgren); Pegel, p. 1012, fig. 10.19.

2003 *Tomagnostus fissus* (Linnarsson, 1879); Axheimer and Ahlberg, p. 150, figs. 7 D–F.

2006 *Tomagnostus fissus* (Lundgren *in* Linnarsson, 1879); Fletcher, pp. 66–67, pl. 34, figs. 41–42.

2008 *Tomagnostus fissus* (Lundgren in Linnarsson 1879); Høyberget and Bruton, p. 64, pl. 11, figs. F–G.

? 2008 *Tomagnostus fissus*; Laurie, pp. 212–213, pl. 1, figs. 35–36.

2009 *Tomagnostus fissus* (Linnarsson, 1879); Weidner and Nielsen, p. 262, fig. 12 A.

2014 *Tomagnostus fissus* (Lundgren in Linnarsson, 1879); Weidner and Nielsen, pp. 21–22, figs. 19 A–D.

Diagnosis. Moderately scrobiculate genae; anterior glabellar lobe with frontal sulcus variable prolonging into pre-glabellar field; elongate cepahlic axial node from midpoint of posterior glabellar lobe along to F3 furrow; glabellar F3 furrow strongly curved anteriorly; pygidium with long lanceolate shaped axis; secondary median node on posteroaxis next to F2 furrow developed (based on Westrop *et al.*, 1996; and Høyberget and Bruton, 2008, with modifications).

Neotype. Specimen no. SGU 4840, Swedish Geological Survey, Uppsala, Sweden, by subsequent designation of Westergård (1946, p. 58, pl. 7, fig. 22), refigured by Whittington *et al.* (1997, fig. 224. 3a). According to Westergård (1946), the holotype is lost.

Material. Two complete specimens, 56 cephala and 23 pygidia (NFM F-1651–F-1731) from the lower part (3.78–7.76 m) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland.

Description. The specimens are poorly to well preserved. The complete specimens are 4 mm and 7.9 mm long, respectively. The size of the cephala varies from 0.9 to 4.1 mm in width and from 1.1 to 3.9 mm in length. The size of the pygidia varies from 2.0 to 3.1 mm in width and from 2.0 to 2.9 in length. Some of the specimens show a yellow surface, typical and natural from the pyrite in the shales of the formation.

The smaller specimens, meraspis stage, have smooth to weak scrobiculate cephalic genae. All the larger specimens show moderately developed scrobicules. Some of the larger specimens have a well-developed frontal sulcus, which may extend into the pre-glabellar field. The typical elongate cephalic axial node is visible in all specimens, with the F3 furrow strongly curved anteriorly. The pygidial secondary median node and the depressed pygidial posteroaxis are visible in some specimens. This is possibly a matter of preservation.

Discussion. This species is easily distinguished from closely related species by its subelliptical to subquadrate cephalon and pygidium (Westergård, 1946; Weidner and Nielsen, 2014). The anterior glabellar lobe has a frontal sulcus developed, that often extends into the pre-glabellar field. Another characteristic feature is the glabellar F3 furrow, which is strongly curved anteriorly (Høyberget and Bruton, 2008).

The closely related species *Tomagnostus perrugatus* (Grönwall, 1902) differs by its strong scrobiculate cephalic genae, with often a crescentic pair of furrows situated opposite the anterior glabellar lobe (Weidner and Nielsen, 2014). Both species show a depressed pygidial posteroaxis, but *T. perrugatus* also has a pair of pygidial posterolateral spines developed.

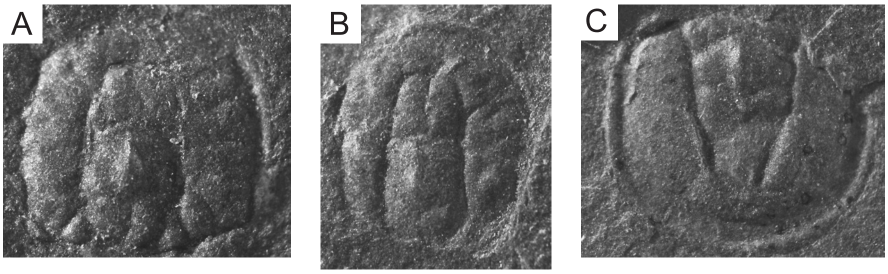


Fig. 22: Tomagnostus fissus (Lundgren in Linnarsson, 1879); **A**, cephalon (NFM F-1651), ×10; **B**, cephalon (NFM F-1652), ×10; **C**, pygidium (NFM F-1653), ×10.

Linnarsson (1879) defined *T. fissus* and described the characteristic scrobiculation on the cephalic genae. In his view, the scrobiculation on the specimens at hand was too faint; thus, his figured cephalon is smooth. Matthew's (1896) subspecies *Agnostus fissus trifissus* is distinguished from *T. fissus* by two additional furrows at the front of the anterior glabellar lobe, parallel to the frontal sulcus. Because of the considerable variability of the development of the scrobicules on the cephalon, the subspecies *trifissus* is here considered merely an intraspecific variation. An example of the the variation of these cephalic srobiculate furrows is shown by Robison (1994, fig. 30.4).

Samson *et al.* (1990) figured a poorly preserved cephalon and two pygidia, which are here tentatively assigned to *T. fissus*. In the synonymy list of Rudolph (1994), *Agnostus fissus* (pl. 16, fig. 10) of Matthew (1896) was listed. This was actually a figure of the subspecies *Agnostus fissus* var. *trifissus*. Furthermore Rudolph (1994) listed *Triplagnostus fissus* of Shergold *et al.* (1990) in his synonymy list, although the description refers to *Tomagnostus fissus*. Westrop *et al.* (1996) assigned the species to the subgenus *Ptychagnostus* (*Ptychagnostus*) in a very wide sense, which means he assigned rather variable forms to *fissus*.

The figured cephalon of Laurie (2008) does not show the characteristics of *T. fissus*. The cephalon has no scrobicules, the frontal sulcus is small and faint and the glabellar F3 furrow is not curved anteriorly. Because of this, the assignment to *T. fissus* is here considered questionable.

Occurrence. *Tomagnostus fissus* is a common and widespread species in the middle Cambrian (global *Ptychagnostus gibbus* Zone to the upper *Ptychagnostus atavus* Zone) of Canada (Newfoundland), USA (Massachusetts and South Carolina), England, Scotland, Sweden, Denmark, Norway, Germany (in erratic boulders), Greenland and Siberia.

Tomagnostus perrugatus (Grönwall, 1902)
(Text-figs. 23 A–C)

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

? 1915 *Agnostus fissus*, var. *perrugatus* Grönwall; Illing, p. 407, pl. 28, fig. 9.

1915 *Agnostus sulcatus*, sp. nov. Illing, p. 411–412, pl. 30, figs. 3–6.

1946 *Tomagnostus perrugatus* (Grönwall, 1902); Westergård, pp. 59–60, pl. 8, figs. 1–10.

1962 *Tomagnostus perrugatus* (Groenwall); Hutchinson, p. 77, pl. 7, figs. 6–9.

1979 *Tomagnostus perrugatus* (Grönwall 1902); Rushton, pp. 55–56, figs. 6 C–E.

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

1982 *Tomagnostus perrugatus* (Grönwall, 1902); Egorova *et al.*, p. 59, pl. 17, figs. 5–6; pl. 54, figs. 9, 12.

pars 1982 *Tomagnostus deformis* Prokovskaya, 1958; Egorova *et al.*, p. 60, pl. 5 fig. 5 (not pl. 8, fig. 9; pl. 12, fig. 13).

1988 *Tomagnostus perrugatus* (Grönwall, 1902); Martin and Dean, p. 17, pl. 3, fig. 2.

1992 *Tomagnostus* cf. *perrugatus* (Grönwall, 1902); Fatka and Kordule, p. 60, pl. 2, fig. 3.

1994 *Tomagnostus perrugatus* (Grönwall, 1902); Robison, p. 60, figs. 31.1–3.

1994 *Tomagnostus perrugatus* (Grönwall 1902); Rudolph, pp. 128–129, pl. 8, fig. 14.

2008 *Tomagnostus perrugatus*; Laurie, pp. 212–213, pl. 1, figs. 37–38.

2014 *Tomagnostus perrugatus* (Grönwall, 1902); Weidner and Nielsen, pp. 22–23, figs. 20 A–F.

Diagnosis. Strong scrobiculate genae and small pits next to the border; anterior glabellar lobe with frontal sulcus; crescentic pair of furrows located opposite the anterior glabellar lobe; pygidium rounded to pentagonal; lanceolate pygidial axis; pygidial pleural fields with small pits; pair of pygidial posterolateral spines (based on Robison, 1994, with modifications).

Holotype. Specimen no. MGUH 143, Geological Museum, University of Copenhagen, Denmark, by original designation of Grönwall (1902, p. 50, pl. 1, fig. 1) and refigured by

Weidner and Nielsen (2014, p. 22, fig. 20 A).

Material. 21 complete specimens, 105 cephala and 89 pygidia (NFM F-1732–F-1946) from the level 2.71–14.97 m of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

Description. The specimens are well preserved. The complete specimens are varying from 4.3 to 11.0 mm in length. The size of the cephala varies from 2.1 to 4.9 mm in width and from 2.1 to 5.4 mm in length. The size of the pygidia varies from 2.0 to 6.2 mm in width and from 2.2 to 6.3 in length.

All cephala have strong scrobiculate genae and a crescentic pair of furrows located opposite the anterior glabellar lobe. The frontal sulcus at the anterior glabellar lobe may extend into pre-glabellar field such as a median preglabellar furrow. Some larger specimens show small pits on the genae along the border furrow. Pygidia have a characteristic rounded to pentagonal outline with a curved to tapered pygidial margin in between the posterolateral spines. The transverse depression near midlength of the posteroaxis is well developed. The nodes on M2 are prominently exposed. All pygidia show the posterolateral spines.

Discussion. This species is easily distinguished from the closely related *Tomagnostus fissus* (Lundgren in Linnarsson, 1879) by rounded cephala and pygidia, strong scrobiculate cephalic genae, crescentic pair of furrows opposite the anterior glabellar lobe, small pits on the pygidial pleural fields and small pygidial posterolateral spines (Weidner and Nielsen, 2014). Westergård (1946) and Rushton (1979) described different developed pygidia forms depending on the stratigraphic horizon. According to Westergård (1946), specimens from earlier zones may have a pygidial collar, which is situated on the posterior border between the pair of posterolateral spines. Specimens from stratigraphic younger horizons show flat and broad borders and a curved to tapered margin in between the posterolateral spines. Rushton (1979) figured and described all pygidia with the curved posterior border and also some specimens show the pygidial collar. Robison (1994) suggested in his emended diagnosis, that the specimens are without or with pygidial collar. Figs. 31. 2–3 show only pygidia with a curved to tapered margin in between the posterolateral spines. However, specimens of Newfoundland show the curved to tapered margin but without pygidial collars. Therefore the pygidial collar may be an intraspecific variation of *T. perrugatus*.

Grönwall (1902) described and figured the characteristic cephalon with strong scrobiculate genae and the crescentic pair of furrows situated opposite the anterior glabellar lobe. In his view these characters were not adequate to describe a new species. Illing (1915) figured a poorly preserved cephalon, which is here tentatively assigned to *T. perrugatus*. The

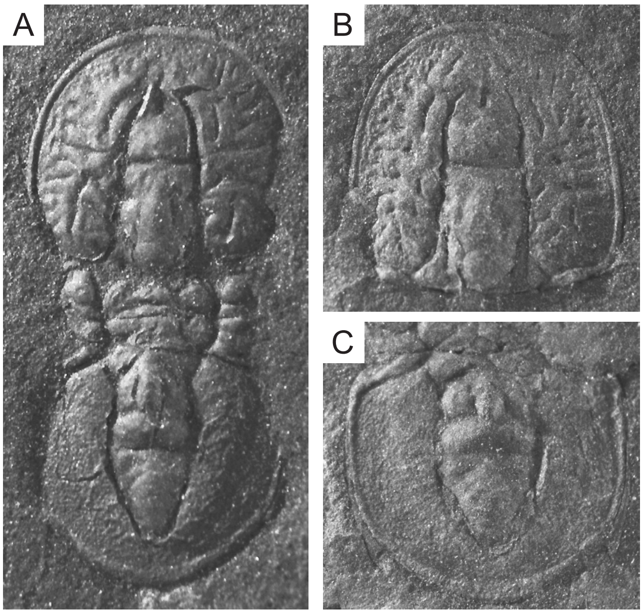


Fig. 23: *Tomagnostus perrugatus* (Grönwall, 1902); **A**, complete specimens (NFM F-1732), ×10; **B**, cephalon (NFM F-1733), ×10; **C**, pygidium (NFM F-1734), ×10.

crescentic pair of furrows may be developed, but the figure is not clearly enough. In addition, Illing (1915) defined the new species *Agnostus sulcatus*. The four complete specimens all show typical characters of *T. perrugatus* such as cephalic scorbiculate genae, the frontal sulcus and the crescentic pair of furrows next to the anterior glabellar lobe. The pygidia have the characteristic rounded to pentagonal margin with a broad border, pits on the pleural fields and the pair of posterolateral spines. Fig. 4 may show a pygidial collar, but the specimen is too poor preserved. Because all of these characters it is here suggested to be a synonym of *T. perrugatus*.

Fatka *et al.* (1981) assigned his three figured cephala to the species *Tomagnostus renata*. The figures and the description agrees well with *T. perrugatus*. The main distinguishing characters for Fatka *et al.* (1981) are different scrobiculae on the cephalon, which are not visible on the figures. Thus, the specimens are here assigned to be a synonym. Egorova *et al.* (1982) described *Tomagnostus deformis* and figured three specimens. Pl. 5 fig. 5 is a complete specimens, which shows all characteristics of *T. perrugatus*. The two other specimens are too poorly preserved, thus an assignment to any species is questionable.

Occurrence. *Tomagnostus perrugatus* is previously described from Canada (Newfoundland and New Brunswick), Greenland, England, Sweden, Denmark, Germany (in erratic boulders), Czech Republic and Siberia. The stratigraphic occurrence of *T. perrugatus* has a wide range from the global *Ptychagnostus gibbus* Zone to the *Ptychagnostus punctuosus* Zone (Rushton, 1979; Robison, 1994).

Superfamily Condylopygoidea Raymond, 1913
Family Condylopygidae Raymond, 1913
Genus *Pleuroctenium* Hawle and Corda, 1847

Type species. *Battus granulatus* Barrande, 1846, by original designation.

Diagnosis. Large anterior glabellar lobe crescentic, enclosing the posterior glabellar lobe; cephalic and pygidial borders and border furrows narrow; surface granular; spines developed; discrete spines from axial pygidial nodes (based on Shergold *et al.*, 1990; Whittington *et al.*, 1997, with modifications).

Synonyms. *Dichagnostus* Jaekel, 1909.

Remarks. The genera of the superfamily Condylopygoidea are the most morphologically differentiated members of the Order Agnostida (Shergold *et al.*, 1990; Naimark, 2012). The typical characte, that differentiate Condylopygoidea from Agnostoidea are the expansion of the anterior glabellar lobe, absence of basal lobes and the presence of three segments in the pygidial anteroaxis. In addition, as also described by Rushton (1966; 1979) the Condylopygoidea are characterised by their variable spines on cephala and pygidia. The superfamily contains a single family Condylopygidae and two genera, *Condylopyge* and *Pleuroctenium* (Shergold *et al.*, 1990).

Pleuroctenium is easily distinguished from *Condylopyge* by the cephalic and pygidial narrower border furrows, the granular surface and the large crescentic anterior glabellar lobe, which encloses the posterior glabellar lobe. By contrast, *Condylopyge* has also a large anterior glabellar lobe, but the shape is semicircular and therefore the lobe does not surround the posterior glabellar lobe.

Pleuroctenium granulatum (Barrande, 1846)
(Text-figs. 24 A–B)

1846 *Battus granulatus* Barrande, p. 15–16.

1847 *Pleuroctenium granulatum*, nob.; Hawle and Corda, pp. 116–117, pl. 6, fig. 63.

1852 *Agnostus granulatus* Barrande; Barrande, p. 911, pl. 49, figs. 1 a–7.

1862 *Agnostus granulatus*; Suess, p. 530, fig. 6.

1908 *Agnostus granulatus* Barr.; Gürich, p. 16, pl. 3, fig. 3.

1909 *Dichagnostus granulatus* Barr; Jaekel, pp. 396–397, fig. 13.

1915 *Agnostus granulatus* Barrande; Illing, p. 419, pl. 32, figs. 11–13.

1939 *Pleuroctenium granulatum* Barrande, 1846; Kobayashi, pp. 109–110, fould-out chart in appendix.

1946 *Pleuroctenium scanense* sp. n. Westergård, pp. 35–36, pl. 2, figs. 14–17.

pars 1958 *Pleuroctenium granulatum* (Barrande, 1846); Šnajdr, pp. 56–59, pl. 2, figs. 5, 7–13 (not 14–15).

1959 *Pleuroctenium granulatum* (Barrande); Harrington *et al.*, p. 174, fig. 112.3.

1962 *Pleurectinium granulatum* (Barrande); Hutchinson, pp. 66–67, pl. 4, figs. 10 a–14.

? 1963 *Pleuroctenium granulatum* (Barrande); Smith and White, pp. 400–401, pl. 57, figs. 5–9.

1966 *Pleuroctenium granulatum granulatum* (Barrande); Rushton, pp. 32–33, text-fig. 13 b.

1966 *Pleuroctenium granulatum scanense* Westergård; Rushton, pp. 32–33, text-fig. 13 c.

non 1966 *Pleuroctenium granulatum pileatum* subsp. nov. Rushton, pp. 32–33, text-fig. 13 a, pl. 4, figs. 18–24.

1970 *Pleuroctenium granulatum* (Barrande, 1846); Horný and Bastl, pl. 1, fig. 6.

? 1979 *Pleuroctenium granulatum granulatum* (Barrande 1846); Rushton, pp. 46–47, figs. 2 A–B.

1979 *Pleuroctenium granulatum scanense* Westergaard 1946; Rushton, pp. 47–48, figs. 2 J–K.

1990 *Pleuroctenium granulatum granulatum* (Barrande, 1846); Shergold *et al.*, pp. 92–93, fig. 19.3 a.

1990 *Pleuroctenium granulatum* (Barrande, 1846) *scanense* Westergård, 1946; Shergold *et al.*, pp. 92–93, fig. 19.3 b.

1997 *Pleuroctenium granulatum scanense*; Whittington *et al.*, p. 382, fig. 240.4 a.

1997 *Pleuroctenium granulatum* (Barrande); Whittington *et al.*, p. 382, fig. 240.4 b.

2004 *Pleuroctenium granulatum granulatum* (Barrande, 1846); Fatka *et al.*, p.

77, pl. 1, fig. 1, text-fig. 2.
2006 *Pleuroctenium granulatum scanense* Westergård, 1946; Fletcher, pp. 66–67, pl. 34, figs. 45–46.

Diagnosis. Anterior glabellar lobe with variable frontal sulcus; axial node on posterior glabellar lobe next to posterior border; pygidial axis broad and rounded posteriorly; lateral pygidial border and spines serrated; pygidial posterolateral spines variable in length.

Lectotype. Specimen no. ČC 250, NMP 1008, National Museum of Prague, Prague, Czech Republic, by subsequent designation of Šnajdr (1958, pl. 2, fig. 5), originally illustrated by Barrande (1852, pl. 49, figs. 5–7).

Material. 20 cephala and 9 pygidia (NFM F-1947–F-1975) from almost the complete Manuels River Formation (2.12–15.46 m) type locality, Conception Bay South, Newfoundland, Canada. Most specimens (15 cephala and 7 pygidia) were sampled from the interval 12.26–15.46 m of the section.

Description. The specimens are mainly poorly preserved, but often the cephala and pygidia are fragmentary. The size of the cephala varies from 0.6 to 2.6 mm in width and from 0.7 to 2.8 mm in length. The size of the pygidia varies from 1.4 to 2.9 mm in width and from 1.5 to 3.3 mm in length.

Most specimens, especially the cephala, are very small. By contrast, the pygidia are larger in intersection, as described above. These variations might represent different ontogenetic stages. The anterior glabellar lobe carries a frontal sulcus and the axial node is situated at the posterior part of the lobe. The cephalic and pygidial borders are narrow. All pygidia show a broad and rounded axis with three pairs of lateral furrows and nodes. The lateral borders of the pygidia are serrated. One fragmentary pygidium shows a long posterolateral spine. All other pygidia have short spines, which might be a matter of preservation. In addition, all cephala and pygidia show a granular surface.

Discussion. *Pleuroctenium granulatum* shows strong morphological variations within populations (Rushton, 1966; Rushton, 1979). The anterior glabellar is in some specimens rounded anteriorly and truncate in other specimens. The rounded anterior lobe is interrupted by a frontal sulcus. Other specimens have a median lateral furrow through the lobe and variable in depth (Rushton, 1966). Also a small spine next to the axial node and posterolateral cephalic spines are variably developed or absent. A pair of pygidial posterolateral spines

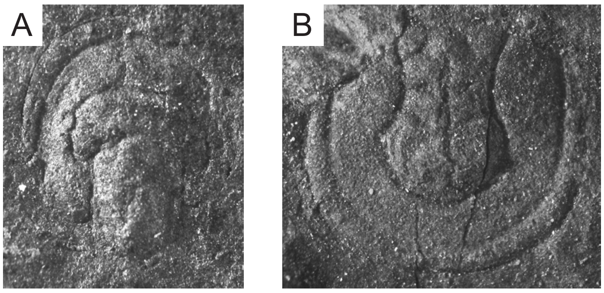


Fig. 24: *Pleucroctenium granulatum* (Barrande, 1846); **A**, cephalon (NFM F-1947), ×15; **B**, pygidium (NFM F-1948), ×15.

are always present and variable in length. Fatka *et al.* (2004) described the serrated lateral margin of the pygidia and the spines. Between c. 22 to 30 small spines occur on each side of the margin.

The closely related species *P. bifurcatum* differs from *P. granulatum* in having a rounded anterior glabellar lobe in front and a long median spine on the posterior thoracic segment, which extends backwards across the pygidial axis (Rushton, 1979). In addition, the pygidial axis of *P. bifurcatum* is slender, in contrast to the broad axis of *P. granulatum*. Neither the lateral border, nor the spines are serrated in *P. bifurcatum*.

P. tuberculatum is distinguished from *P. granulatum* by a very small anterior glabellar lobe, which is rounded anteriorly. The posterior glabellar lobe of *P. tuberculatum* is ovate and slender. The pygidial posteroaxis is shorter than that of *P. granulatum* (Rushton, 1966). In addition, the lateral serration of the pygidial border and spines is absent in *P. tuberculatum*.

Hawle and Corda (1847) described the new genus *Pleuroctenium* to which they assigned the species *P. granulatum*. Jaekel (1909) described the new species *Dichagnostus* on the basis of characters such as large anterior glabellar lobe with a furrow, a broad threepartite pygidial axis and pygidial spines. In addition, Jaekel's (1909) illustration of *P. granulatum* shows a serrated lateral margin of the pygidia and the spines. Because of the described and figured characters it is here assigned to *P. granulatum*.

Westergård (1946) described the new species *P. scanense* on the basis of two chephala and four pygidia. He remarked, that the specimens were too poorly preserved for a detailed description. Nevertheless, Westergård (1946) concluded that this species is distinguished from *P. granulatum* by a deeper frontal sulcus of the anterior glabellar lobe, a slender pygidial posteroaxis and a shorter pair of pygidial posterolateral spines. By contrast, the figured specimens show the typical characters of *P. granulatum*. In addition, the above described differences are here suggested to be intraspecific variations and therefore this species is considered a synonym of *P. granulatum*.

The specimen of Šnajdr (1958, fig. 14) is poorly and fragmentarily preserved, so an assignment to this species is suggested to be doubtful. A complete specimen Šnajdr (1958, fig. 15) shows an anteriorly rounded anterior glabellar lobe, cephalic spines and a slender pygidial axis, characters that are typical of *P. bifurcatum*. Hutchinson (1962) misspelled the genus *Pleurectinium* and provided no description. The figured specimens of Smith and White (1963) are poorly preserved and the assignment to *P. granulatum* is considered questionable.

Because of the wide intraspecific variations of *P. granulatum* the concept of Rushton (1966) to divide the species into three subspecies was followed by several authors. Rushton (1966) characterised *P. granulatum granulatum* by the truncate anterior glabellar lobe with a median lateral furrow and the serration at the pygidial lateral margin down to the long spines. Later, Rushton (1979), Shergold *et al.* (1990) and Fatka *et al.* (2004) followed the subspecies concept of Rushton (1966).

The subspecies *P. granulatum scanense* of Rushton (1966), which was first described by Westergård (1946), was characterised by a frontal sulcus visible at the anterior glabellar lobe, short pygidial posterolateal spines and serration at the lateral pygidial margin. Later, Rushton (1979), Shergold *et al.* (1990), Whittington *et al.* (1997) and Fletcher (2006) followed the subspecies concept of Rushton (1966). Here, it is suggested that the characters described by Rushton (1966) and the figured specimens from the studies listed above are merely intraspecific variations.

The third subspecies of Rushton (1966), *P. granulatum pileatum*, was characterised by a rounded anterior glabellar lobe, long pygidial posterolateral spines and the absence of serration on the pygidial lateral margin. In addition, the figured specimens show also a slender pygidial axis. Therefore, this subspecies is here suggested to be a synonym of *P. bifurcatum*.

Occurrence. *Pleuroctenium granulatum* occurs in the middle Cambrian (global *Ptychagnostus atavus* Zone) of eastern Canada (Newfoundland), Wales, England, Sweden and the Czech Republic.

Suborder Eodiscina Kobayashi, 1939
Superfamily Eodiscoidea Raymond, 1913
Family Eodiscidae Raymond, 1913
Genus *Eodiscus* Hartt *in* Walcott, 1884

Type species. *Eodiscus pulchellus* Hartt *in* Walcott, 1884, by original designation, a junior synonym of *Microdiscus scanicus* Linnarsson, 1882.

Diagnosis. Median preglabellar furrow; glabella anteriorly tapered; glabellar and occipital furrows deep; occipital cephalic spine; eyes and facial sutures absent; thorax with three segments; pygidium with long and narrow axis; axis segmented by several rings; variable surface ornamentation (based on Rasetti, 1952; Whittington *et al.*, 1997, with modifications).

Synonyms. *Microdiscus* Salter, 1864a; *Spinodiscus* Kobayashi, 1943; *Deltadiscus* Kobayashi, 1943.

Remarks. *Microdiscus scanicus* Linnarsson, 1882, the type species of *Eodiscus*, was originally described from Andrarum, Scania, Sweden.

Eodiscus is easly distinguished from other genera of Eodiscidae by the deep median preglabellar furrow, the narrow cephalic border, the absence of eyes; a strong occipital spine and the pygidial axis with several segmented rings. *Serrodiscus* differs from *Eodiscus* by ventral spines situated along the pygidial border, which are absent in *Eodiscus*. *Dawsonia* is distinguished from *Eodiscus* by a coarse crenulation of the cephalic border, the absence of a median preglabellar furrow, two thoracic segments and the shorter pygidial axis with only six segments (Rasetti, 1952; Whittington *et al.*, 1997).

Nevertheless, the systematic position of eodiscid trilobites is still under discussion. Babcock (1994) assigned Eodiscidae to be doubtful because of the phylogenetic status. Axheimer and Ahlberg (2003) classified the order as uncertain without any remarks.

By contrast, the order of Agnostida is described by the matching outline of pygidium and cephalon, glabella widest at posterior end and two or three thoracic segments (Harrington *et al.*, 1959; Whittington *et al.*, 1997). Therefore, here it is followed this concept to assign all genera of Eodiscidae to the order Agnostida.

Eodiscus punctatus (Salter, 1864b)

(Text-figs. 25 A–C)

1864 *Microdiscus punctatus*, sp. nov. Salter, pp. 237–238, pl. 13, figs. 11 a–c.
1882 *Microdiscus eucentrus* n. sp. Linnarsson, pp. 30–31, pl. 4, figs. 19–20.
pars 1884 *Microdiscus punctatus*, Salter; Walcott, pp. 24–25, pl. 2, figs. 1 c (not 1–1 b).
? 1886 *Microdiscus punctatus*, var. *precursor*, n. var. Matthew, p. 75, pl. 7, fig. 13.
non 1886 *Microdiscus punctatus* (Salter), var. *pulchellus*, Hartt; Matthew, pp. 74–75, pl. 7, figs. 12 a–c.

pars 1907 *Microdiscus punctatus*, Salter; Lake, pp. 36–39, pl. 3, figs. 11–15 (not 16–17 a).

1911 *Microdiscus* sp., cf. *M. punctatus* Salt.; Cobbold, p. 292, pl. 25, figs. 12 a–c.

non 1913 *Eodiscus punctatus* (Salter); Raymond, p. 103, fig. 1.

1915 *Microdiscus punctatus* Salter; Illing, p. 423, pl. 33, figs. 9–10.

non 1915 *Microdiscus punctatus*, var. *scanicus* Linnarsson; Illing, pp. 423–424, pl. 33, figs. 11 a–12.

1944 *Spinodiscus punctatus* Salter; Kobayashi, p. 55, pl. 1, fig. 7.

1946 *Eodiscus punctatus* (Salter, 1864); Westergård, pp. 24–25, pl. 1, figs. 12–15.

1952 *Eodiscus punctatus* (Salter); Hutchinson, p. 73, pl. 1, figs. 13–16.

1952 *Eodiscus punctatus* (Salter); Rasetti, pp. 448–449, pl. 53, figs. 1–6.

1959 *Eodiscus punctatus* (Salter); Harrington *et al.*, p. 187, figs. 129.1 a–b.

1962 *Eodiscus punctatus* (Salter); Hutchinson, p. 59, pl. 2, figs. 3–7.

1962 *Eodiscus scanicus* (Salter); Hutchinson, p. 59, pl. 2, figs. 1 a–2 c.

pars 1969 *Eodiscus punctatus* (Salter, 1864); Poulsen, p. 3, fig. 2 B (not 2 A).

pars 1982 *Eodiscus punctatus* (Salter, 1864); Egorova *et al.*, p. 57, pl. 4, fig. 8; pl. 12, fig. 2; pl. 51, fig. 10; pl. 55, fig. 15 (not pl. 7, fig. 7; pl. 51, fig. 9).

non 1982 *Eodiscus* cf. *E. punctatus scanicus* (Linnarsson); Kindle, pp. 4–5, pl. 1.2, figs. 5, 9.

1988 *Eodiscus punctatus* (Salter, 1864) *scanicus* (Linnarsson, 1883); Martin and Dean, p. 15, pl. 1, figs. 8–9.

1994 *Eodiscus punctatus* (Salter 1864); Rudolph, pp. 157–158, pl. 11, figs. 4–7.

? 2006 *Eodiscus punctatus* (Salter 1864); Fletcher, pp. 66–67, pl. 34, fig. 32.

2008 *Eodiscus punctatus* (Salter 1864); Høyberget and Bruton, pp. 72–73, pl. 12, figs. N–R.

? 2014 *Eodiscus punctatus* (Salter, 1864); Weidner and Nielsen, pp. 45–46, figs. 40 A–F.

Diagnosis. Deep median preglabellar furrow; wide cephalic border; cephalic genae and pygidial pleural fields convex; long occipital cephalic spine; pygidial axis segmented in seven to nine rings.

Lectotype. Specimen no. BMNH 42646, Natural History Museum, London, United Kingdom, by subsequent designation of Morris (1988, p. 91), originally figured by Salter (1864b).

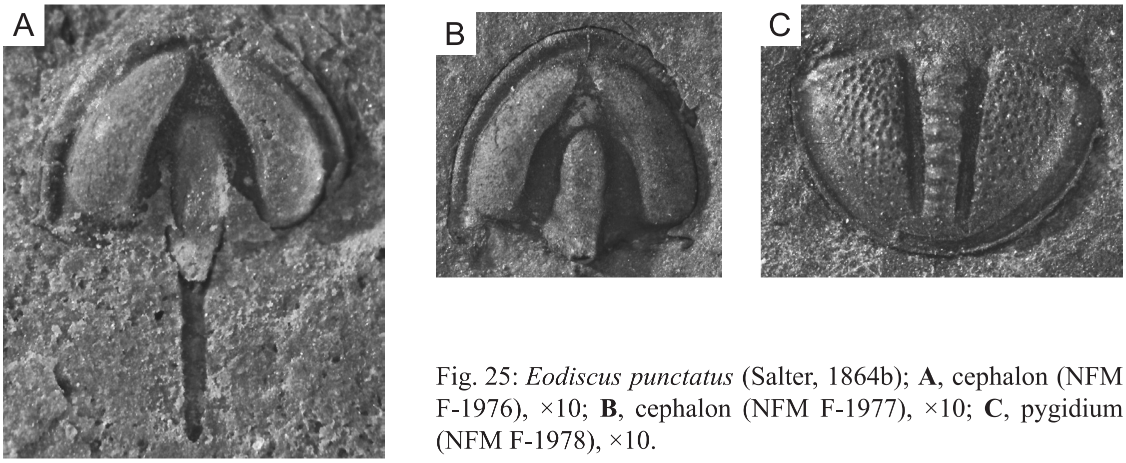


Fig. 25: *Eodiscus punctatus* (Salter, 1864b); **A**, cephalon (NFM F-1976), ×10; **B**, cephalon (NFM F-1977), ×10; **C**, pygidium (NFM F-1978), ×10.

Material. Two complete specimens, 215 cephala and 213 pygidia (NFM F-1976–F-2405) of the levels 2.24–16.71 m of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

Description. The specimens are mainly well preserved. The complete specimens, preserved as moulds, are 7.8 mm and 8.8 mm long, respectively. The size of the cephala varies from 2.2 to 3.9 mm in width and from 1.6 to 3.6 mm in length. The size of the pygidia varies from 2.2 to 4.2 mm in width and from 1.9 to 3.9 mm in length. Some specimens show a yellow surface from the containing pyrite in the shales.

All cephala and pygidia are broad rather than long. The cephala are mainly tapered anteriorly, in some cases they are more rounded. The cephala and pygidia have a semiovate shape. The cephalic border shows fine radiating furrows, which are often better preserved in moulds than on positive specimens. All specimens show deep median preglabellar furrows and glabellar furrows, respectively. The cephalic occipital spine is in most specimens long visible, in others the spine is broken, which is probably a matter of preservation. The surface of the cephalic genae and the pygidial pleural fields varies from nearly smooth to strong punctate. The larger specimens often show the strongest punctation. All specimens have the characteristic convex shape of the genae and the pleural fields. The pygidial axis have deep axial furrows and seven to, mainly, nine rings.

Discussion. *Eodiscus punctatus* shows many morphological intraspecific variations and variations throughout ontogeny (Lake, 1907; Westergård, 1946; Rasetti, 1952; Høyberget and Bruton, 2008; Weidner and Nielsen, 2014). The fine radiating furrows on the cephalic border vary from very faint to well developed. The surface ornamentation of the cephala and pygidia is varying from smooth punctate to strongly punctate and is therefore not appropriate as a characteristic of the species *E. punctatus* (Westergård, 1946; Rasetti, 1952). It also varies during different ontogentic stages from fainter in meraspids to stronger in holaspids. The occipital spine is in some specimens longer, in others shorter visible. In addition, the angel of the spine varies from c. 20–45° (Westergård, 1946; Weidner and Nielsen, 2014). Because of the length, the slenderness and the angel, the spine is in some specimens broken, what is probably a matter of preservation. In the past only the length and also the angle of the spine were used to distinguish *E. punctatus* from *E. scanicus* (Rasetti, 1952; Hutchinson, 1962; Poulsen, 1969). Because the spines are often broken, so the angle is not a reliable character, later, several other characters were used for distinguishing these species, which is followed here.

E. punctatus is distinguished from the closely related species *E. scanicus* by the wider cephalic border, the deep median preglabellar furrow, the deep and broader axial furrows and the longer occipital spine. Further, *E. punctatus* differs in the more convex shape of the cephalic genae and pygidial pleural fields and the number of the pygidial axial rings from seven to nine segments. By contrast, *E. scanicus* shows ten or more pygidial axial rings (Rasetti, 1952; Høyberget and Bruton, 2008; Weidner and Nielsen, 2014).

Linnarsson (1882) described the species *Microdiscus eucentrus*. He figured a cephalon and a pygidium, which both show the characteristic punctate surface of *E. punctatus*. The cephalon has a long occipital spine and deep axial furrows. The pygidium shows a long and narrow axis segmented by nine rings. All these described characters are typical for *E. punctatus*, thus the species *M. eucentrus* is here considered a synonym. Walcott (1884) figured three cephala and a single pygidium of *Microdiscus punctatus*. The pygidium shows the charactristics of *E. punctatus* such as a pygidial axis with nine rings and convex pygidial pleural fields. All cephala show a broad glabella with a short spine. In addition, two of the cephala have tubercles along the cephalic border. These described characters do not agree with *E. punctatus*, thus the three cephala are here not assigned to this species.

Matthew (1886) described the subspecies *M. punctatus precursor*. He figured a single cephalon with an ogival shaped cephalon and a broad glabella without an occipital spine. The median preglabellar furrow and the axial furrows are broad and deep visible. Because the characteristic occipital spine is absent and there is no pygidial illustration of the subspecies the assignment to *E. punctatus* is here considered questionable. Furthermore, Matthew (1886) descbribed the subspecies *M. punctatus pulchellus*. He figured a cephalon, a side view of a cephalon and a pygidium. The cephalon shows a narrow median preglabellar furrow and narrow axial furrows, the occipital spine is as long as the glabella. The cephalon has a narrow pygidial axis, which is segmented by eleven rings. Therefore, the subspecies is assigned to *E. scanicus*.

Lake (1907) illustrated two complete specimens and four cephala of the species *M. punctatus*, which all match well with *E. punctatus*. Further, he figured three pygidia which show a long and narrow pygidial axis segmented by ten rings. The pygidial pleural fields are not as convex as those of *E. punctatus* and one of the pygidia has a smooth surface. In addition, Lake (1907) marked intraspecific variations and assigned all his specimens to one species. The figured pygidia on figs. 16–17 a are here assigned to *E. scanicus*. Cobbold (1911) sampled scattered pygidia and he was therefore not cetrain about the assignment to *E. punctatus*. The illustrated pygidia show the typical characters of *E. punctatus* such as long narrow pygididal axis with seven ring segments.

Raymond (1913) illustrated a complete specimen of *E. punctatus*, showing a cephalon with tubercles along the cephalic border, narrow axial furrows and a short occipital spine. These characters are not specific for this species, thus Raymond's (1913) specimens is here not assigned to *E. punctatus*. Illing (1915) figured three complete specimens of the subspecies *M. punctatus scanicus*. They all show a faint median preglabellar furrow and eleven rings on the pygidial axis, typical for *E. scanicus*. Kobayashi (1944) assigned his figured complete specimen to his new described genus *Spinodiscus*. He assigned *M. punctatus* as the type species of the new genus. As also marked in the genus *Eodiscus* (see Chapter Eodiscus) *Spinodiscus* is here considered a synonym of the former.

Hutchinson (1962) illustrated three cephala and pygidia of *E. scanicus*. These figures show exactly the same characters as his figures of *E. punctatus*. In addition, Hutchinson (1962) wrote, that the two species are very similar and they show intermediate forms. Therefore, the figured specimens of *E. scanicus* are considered synonyms of *E. punctatus*. Poulsen (1969) figured a cephalon and a pygidium of *E. punctatus*. The pygidium agrees well with *E. punctatus* but the cephalon shows a faint median preglabellar furrow and the genae are flat. Thus, the cephalon on fig. 2 a is here not assigned to this species.

Egorova *et al.* (1982) figured several specimens of *E. punctatus*. Two cephala have a faint median preglabellar furrows and flat and large genae which are not characteristic for *E. punctatus*. The specimens are here not assigned to this species. The figured cephalon and pygidium of *E. punctatus scanicus* from Kindle (1982) show the typical characters of *E. scanicus* such as faint median preglabellar furrow, a short occipital spine, eleven pygidial axial rings and a smooth surface. Martin and Dean (1988) illustrated specimens of *E. punctatus scanicus*, with specific characters of *E. punctatus*, therefore they are here assigned to this species. Fletcher (2006) figured several specimens on one picture with a resolution that is not appropriate to determine any species. Therefore an assignment to *E. punctatus* is here considered doubtful. Weidner and Nielsen (2014) figured several specimens of *E. punctatus*. Almost all specimens show the typical characters of *E. punctatus* and match therefore well with the species. By contrast, all cephala have a faint median preglabellar furrow, what is typical for *E. scanicus*. Thus the assignment to *E. punctatus* is here suggested to be questionable.

Occurrence. *Eodiscus punctatus* is a common and widespread species in the middle Cambrian (global the lower *Ptychagnostus atavus* Zone to the *Ptychagnostus punctuosus* Zone) of southeast Canada (Newfoundland, New Brunswick and Nova Scotia), Greenland, Wales, England, Sweden, Norway, Denmark, Germany (in erratic boulders) and Siberia.

4. **Biostratigraphy**

4.1. Local biozonation

The lithology of the Manuels River Formation consists of mainly grey to black shales with intercalated calcareous concretions. The result of the cm-by-cm sampling of the section is shown in Fig. 26. The formation has a thickness of 19.00 m (see Austermann, 2016). The basal bed is a 2-cm-thick volcanic ash layer, overlying the greenish shales of the Chamberlain's Brook Formation. Several volcanic ash layers are interbedded at different heights of the succession. Also intercalated concretions occur in different levels. The top of the formation consists of a 7-cm-thick conglomeratic sandstone, which is taken as the basal bed of the overlying Elliot Cove formation. A detailed macro- and microscopic description of the succession is given by Austermann (2016).

The shales are highly fossiliferous throughout the succession. The main taxa are trilobites of the orders Agnostida, Ptychopariida and Redlichiida. The Order Agnostida studied here comprises ten species which are distributed throughout the complete succession. Diversity fluctuates throughout the succession. For detailed occurrences of each species, see Fig. 26.

Five local interval biozones based on agnostoid trilobites are proposed for the Manuels River Formation exposed at the type locality along Manuels River.

4.1.1. ***Peronopsis scutalis*** **Zone**

The base of this zone is defined by the FAD of *P. scutalis* at the stratigraphical height of 1.95 m. The species is common throughout the complete zone and ranges into the following *Tomagnostus fissus* Zone. The assemblage contains *Eodiscus punctatus*, *Pleuroctenium granulatum*, *Hypagnostus parvifrons* and *Tomagnostus perrugatus*. In addition, *E. punctatus* occurs at the base of the zone and is occuring rare in the range of 2.80–2.84 m. The FAD of *P. granulatum* occurs at 2.12 m and the species is rare up to a stratigraphic height of 3.70 m. The FAD of *H. parvifrons* occurs at 2.75 m. The FAD of *T. perrugatus* occurs at 2.71 m and the species is rare up to 2.85 m. The top of the zone is defined by the FAD of *Tomagnostus fissus* at 3.78 m.

4.1.2. ***Tomagnostus fissus*** **Zone**

The base of this zone is defined by the FAD of *T. fissus* at the stratigraphical height of 3.78

m. The species ranges up to 7.76 m and is abundant in the range of 3.78–5.05 m. Additional species at the base of this zone are *Eodiscus punctatus*, *Peronopsis scutalis*, *Pleuroctenium granulatum*, *Hypagnostus parvifrons* and *Tomagnostus perrugatus*. The FAD of *Peronopsis fallax* occurs at the level of 5.91 m. *E. punctatus* is common in the ranges of 5.21–6.00 m, 6.72–7.01 m and 7.51–8.56 m, *P. scutalis* is common in the ranges of 4.04–4.12 m and 4.32–4.53 m, *H. parvifrons* is common in the range of 10.88–11.30 m and at 11.42 m, *T. perrugatus* is abundant at 9.36 m and 10.37 m and in the range of 10.77–11.90 m. The FAD of *P. fallax* is at the stratigraphical height of 5.91 m and the species occurs abundantly in the ranges of 6.72–7.00 m, at 7.13 m, 7.51–7.53 m, at 8.52 m, 9.88–10.20 m and 10.87–11.83 m. *P. granulatum* occurs scattered at 7.00 m and 11.43 m. The LAD of *P. scutalis* occurs at the stratigraphic height of 7.13 m and that of *T. fissus* at 7.76 m. The top of the zone is defined by the FAD of *Ptychagnostus atavus* at the level of 11.90 m.

4.1.3. ***Ptychagnostus atavus* Zone**

The base of this zone is defined by the FAD of *P. atavus* at the stratigraphical height of 11.90 m. The species occurs abundantly throughout the whole occurence up to 12.06 m. The assemblage contains *Eodiscus punctatus*, *Pleuroctenium granulatum*, *Hypagnostus parvifrons*, *Tomagnostus perrugatus* and *Peronopsis fallax*. *E. punctatus* occurs abundant in the ranges of 13.47–14.25 m, *P. granulatum* occurs rare in the ranges of 12.26–12.34 m and 12.42–12.65 m, *T. perrugatus* occurs abundant in the ranges of 11.95 m and 12.26–13.51 m and *P. fallax* occurs abundant in the range of 12.26–14.92 m, *H. parvifrons* occurs scattered at the level 12.62 m. The top of the zone is defined by the FAD of *Ptychagnostus affinis* at the level of 14.92 m.

4.1.4. ***Ptychagnostus affinis* Zone**

The base of this zone is defined by the FAD of *P. affinis* at the stratigraphical height of 14.92 m. The species occurs abundantly througout the whole occurrence up to 15.36 m. Additionally occuring species are *Eodiscus punctatus*, *Pleuroctenium granulatum*, *Hypagnostus parvifrons*, *Tomagnostus perrugatus* and *Peronopsis fallax*. *E. punctatus* occurs abundant in the range of 15.55–16.72 m, *P. granulatum* occurs rare in the range of 15.00–15.31 m, *H. parvifrons* occurs rare in the ranges of 15.10–15.42 m and 15.75–16.11 m and *P. fallax* occurs abundant in the ranges of 14.92–15.45 m and 15.74–16.41 m. The LAD of *E. punctatus* occurs at the stratigraphic height of 16.71 m, that of *P. granulatum* at 15.46 m, that of *H. parvifrons* at 16.17 m, that of *T. perrugatus* at 14.97 m, that of *P. fallax* at 16.41 m and that of *E. punctatus* at 16.71 m. The top of the zone is defined by the FAD of

Ptychagnostus punctuosus at the level of 16.72 m.

4.1.5. ***Ptychagnostus punctuosus* Zone**

The base of this zone is defined by the FAD of *P. punctuosus* at the stratigraphical height of 16.72 m. The species ranges abundantly up to the top of the Manuels River Formation at 19.00 m. The top of the zone is not defined, because the following FAD of a species may occur in the overlying Elliot Cove formation, which is not in the scope of the present study.

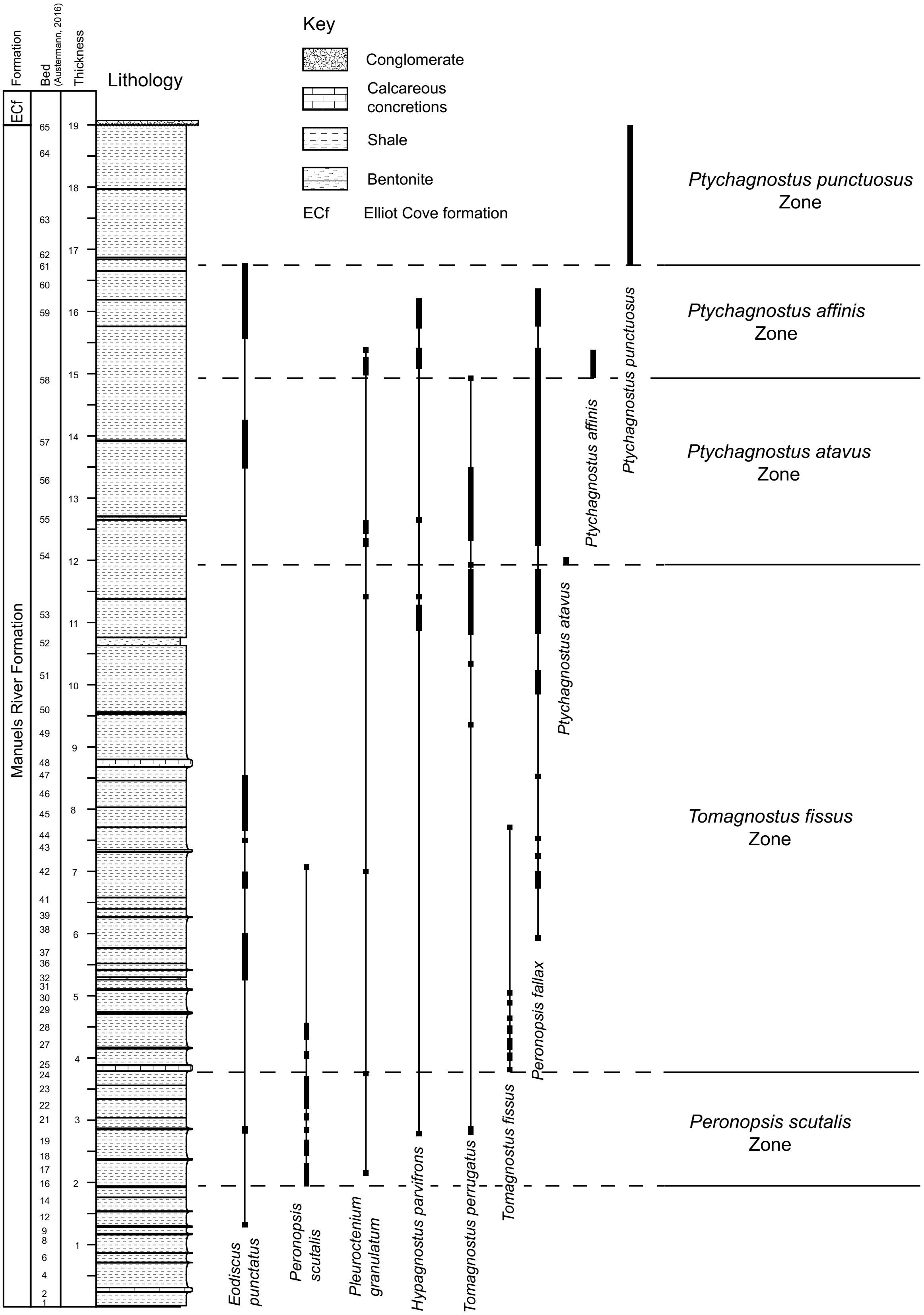


Fig. 26: Lithostratigraphy and agnostoid trilobite biozonation of the middle Cambrian Manuels River Formation at the type locality along Manuels River, Conception Bay South, Newfoundland, Canada.

4.2. Comparison with other regions

Interval biozones are based on the first appearance datum (FAD) of a selected fossil species and are a common tool for chronostratigraphic correlation (Salvador, 1994; Landing *et al.*, 2013). In the middle Cambrian, agnostoid trilobites are frequently used because of their cosmopolitan distribution in open-marine facies, relatively short stratigraphic ranges and abundant occurrence (Robison, 1984, 1994; Peng and Robison, 2000). However, the use of FADs for global chronocorrelation suffers from the inherent diachroneity of the fossil species, the magnitude of which varies between species. Precise correlation is only possible with supplementary information on sedimentology and palaeontology of the correlated area (Landing *et al.*, 2013). The definition of biozones not only requires the designated FAD but also the description of the entire associated faunal assemblage. Several studies of middle Cambrian agnostoid systematics lack in precise definitions of biozones (e.g., Howell, 1925; Westergård, 1946; Egorova *et al.* 1982; Robison, 1984; Westrop *et al.*, 1996; Landing and Westrop, 1998a). Only a few studies deal with definitions *sensu strictu* of local biozones (Fletcher, 1972; Robison, 1994; Peng and Robison, 2000; Weidner and Nielsen, 2014). The faunal assemblage of the biozones of these studies is compared with the present study (Fig. 27). Even with these relatively detailed studies, it is not possible to achieve a precise correlation of the biozones, as information on abundance and precise stratigraphic orrurrence are missing.

The local biozonation presented here is compared with the "global" biostratigraphy of previously published studies. The biozones of the Manuels River Formation are primarily comparable with West Avalonia and supplemented by Baltica, Siberia, southern China and Laurentia (Fig. 28). In the detailed bed-by-bed study of Howell (1925) at the type locality of the Manuels River Formation, the *Paradoxides hicksi* and *Paradoxides davidis* biozones were defined on the basis of the trilobites of the Order Redlichiida, whereas biozones proposed here are based on the Agnostida. Nevertheless, both studies were carried out bed-by-bed, so the biozones of the present study can be compared with Howell's (1925) study based on the stratigraphic level.

	Manuels River, Conception Bay South, Newfoundland											St. Mary's Bay, Newfoundland, Fletcher (1972)				Fosters Point, Newfoundland, Landing and Westrop (1998a)		Cape Breton Island, Nova Scotia, Hutchinson (1952)	
	Present study					Howell (1925)		Hutchinson (1962)		Landing and Westrop (1998a)									
	Peronopsis scutalis Zone	*Tomagnostus fissus* Zone	*Ptychagnostus atavus* Zone	*Ptychagnostus affinis* Zone	*Ptychagnostus punctuosus* Zone	*Paradoxides hicksi* Zone	*Paradoxides davidis* Zone	*Paradoxides hicksi* Zone	*Paradoxides davidis* Zone	*Hydrocephalus hicksi* Zone	*Paradoxides davidis* Zone	*Agraulos longicephalus* Zone	*Agraulos ceticephalus* Zone	*Meneviella venulosa* Zone	*Paradoxides davidis* Zone	*Hydrocephalus hicksi* Zone	*Paradoxides davidis* Zone	*Paradoxides hicksi* Zone	*Paradoxides davidis* Zone
Eodiscus punctatus	r	c	a	a		X	X	X	X		X			X				X	
Peronopsis scutalis	c	c						X	X			X				X	X		
Pleuroctenium granulatum	r	r	r	r		X	X	X	X							X			
Hypagnostus parvifrons	r	c	r	r		X	X	X	X										
Tomagnostus perrugatus	r	a	a	r			X	X	X				X						
Tomagnostus fissus		a				X		X		X		X	X			X			
Peronopsis fallax		a	a	a		X	X	X	X									X	
Ptychagnostus atavus			a					$X^?$	X										
Ptychagnostus affinis				a															
Ptychagnostus punctuosus					a		X		X						X		X		

Fig. 27: Comparison of the West Avalonian biozones and their faunal assemblages with the present study. For the stratigraphic range of the species see Fig. 26. $X^?$: Doubtful occurrence; see discussion of Chapter *Ptychagnostus punctuosus*. occurrence: r=rare , c=common, a=abundant.

	Baltica, Weidner and Nielsen (2014)			Greenland, Robison (1994)	South China, Peng and Robison (2000)	
	lower Ptyachgnostus atavus Zone	*upper Ptyachgnostus atavus* Zone	*Ptychagnostus punctuosus* Zone	*Ptychagnostus atavus* Zone	*Ptychagnostus atavus* Zone	*Ptychagnostus punctuosus* Zone
Eodiscus punctatus		X	X			
Peronopsis scutalis	X	X	X	X		
Pleuroctenium granulatum						
Hypagnostus parvifrons	X	X	X	X	X	X
Tomagnostus perrugatus	X	X		X		
Tomagnostus fissus	X			X		
Peronopsis fallax				X		
Ptychagnostus atavus	X	X	X	X	X	X
Ptychagnostus affinis		X		X	X	
Ptychagnostus punctuosus						X

Fig. 28: Comparison of “global” biozones and their faunal assemblages with the present study (see Fig 27).

<table>
<tr><th colspan="2" rowspan="2"></th><th colspan="4">West Avalonia</th><th rowspan="2">East Avalonia</th><th colspan="2" rowspan="2">Baltica</th><th rowspan="2">Siberia</th><th rowspan="2">South China</th><th rowspan="2">Laurentia</th></tr>
<tr><th>Manuels River, Newfoundland</th><th>Deep Cove, Newfoundland</th><th>Fosters Point, Newfoundland</th><th>Cape Breton Island, Nova Scotia</th></tr>
<tr><td rowspan="8">Drumian</td><td rowspan="8">Manuels River Formation</td><td>*Ptychagnostus punctuosus*</td><td rowspan="4">*Paradoxides davidis*</td><td rowspan="4">*Paradoxides davidis*</td><td rowspan="4">*Paradoxides davidis*</td><td rowspan="4">*Paradoxides davidis*</td><td colspan="2">*Ptychagnostus punctuosus*</td><td rowspan="5">agnostoid zone(s) not named</td><td>*Ptychagnostus punctuosus*</td><td>*Ptychagnostus punctuosus*</td></tr>
<tr><td>*Ptychagnostus affinis*</td><td rowspan="4">*Hypagnostus parvifrons*</td><td rowspan="7">*Ptychagnostus atavus*</td><td rowspan="7">*Ptychagnostus atavus*</td><td rowspan="7">*Ptychagnostus atavus*</td></tr>
<tr><td>*Ptychagnostus atavus*</td></tr>
<tr><td rowspan="3">*Tomagnostus fissus*</td></tr>
<tr><td rowspan="4">*Hydrocephalus hicksi*</td><td rowspan="4">*Hydrocephalus hicksi*</td><td rowspan="4">*Paradoxides hicksi*</td><td rowspan="4">*Hydrocephalus hicksi*</td></tr>
<tr><td rowspan="3">*Tomagnostus fissus*</td><td rowspan="3">*Tomagnostus fissus*</td></tr>
<tr><td>*Peronopsis scutalis*</td></tr>
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Fig. 29: Avalonian and global comparison of the Drumian (middle Cambrian) biozones with the present study. Data base: Deep Cove, Newfoundland (Fletcher, 2006), Fosters Point, Newfoundland (Landing and Westrop, 1998a), Cape Breton Island, Nova Scotia (Hutchinson, 1952), East Avalonia (Rushton, 1979), Baltica (Westergård, 1946 left column; Weidner and Nielsen, 2014 right column), Siberia (Egorova *et al.*, 1982), South China (Peng *et al.*, 2000) and Laurentia (Robison, 1984; Palmer, 1998).

5. Palaeobiogeography

The studied agnostoid fauna occurs mostly abundant and cosmopolitan. An overview of the middle Cambrian occurrence distribution of each agnostoid species is given in Fig. 30.

Peronopsis fallax (Linnarsson, 1869) is cosmopolitan and was reported from the middle Cambrian *Ptychagnostus gibbus* and *Ptychagnostus atavus* zones of e. g. Sweden (Westergård, 1946; Weidner and Nielsen, 2009), North America (Nevada, Utah and South Carolina) (Robison, 1982; Samson *et al.*, 1990), Norway (Høyberget and Bruton, 2008) and Denmark (Weidner and Nielsen, 2014). It was also reported from the upper part of the *Ptychagnostus atavus* Zone of e.g., New Brunswick, Nova Scotia (Hutchinson, 1952), Western Newfoundland (Young and Ludvigsen, 1989), Australia (Öpik, 1979), England (Rushton, 1979), Spain (Gil Cid, 1981), Siberia (Egorova *et al.*, 1982), Eastern Turkey (Dean, 1982), Anatarctica (Palmer and Gatehouse, 1972) and Greenland (Robison, 1994). In the present study *Peronopsis fallax* occurs from the *Tomagnostus fissus* Zone to the *Ptychagnostus affinis* Zone of Eastern Newfoundland.

Peronopsis scutalis (Hicks, 1872) is widespread and was reported from the middle Cambrian *Ptychagnostus gibbus* Zone to the *Lejopyge laevigata* Zone (Robison, 1994; Høyberget and Bruton, 2008; Weidner and Nielsen, 2014). It was noted from the *Ptychagnostus gibbus* Zone of the Northern Territory, Australia (Öpik, 1979), the lower to upper *Ptychagnostus atavus* Zone of Sweden and Greenland (Westergård, 1946; Robison, 1994), the *Ptychagnostus atavus* Zone of Denmark (Weidner and Nielsen, 2014), the *Ptychagnostus atavus* Zone to the lower part of the *Ptychagnostus punctuosus* Zone of Denmark, England, Wales and Norway (Grönwall, 1902; Rushton, 1979; Høyberget and Bruton, 2008) and the *Lejopyge laevigata* Zone of Western Newfoundland (Westrop *et al.*, 1996). In the present study *Peronopsis scutalis* occurs from the *Peronopsis scutalis* Zone to the middle part of the *Tomagnostus fissus* Zone of Eastern Newfoundland.

Hypagnostus parvifrons (Linnarsson, 1869) is a widespread species and was reported from the middle Cambrian lower *Ptychagnostus atavus* Zone of e.g., Öland, Sweden (Weidner and Nielsen, 2009), the *Ptychagnostus atavus* Zone of Sweden and South Carolina, USA (Westergård, 1946; Samson *et al.*, 1990), the upper part of the *Ptychagnostus atavus* Zone of New Brunswick, Québec, Utah, Pennsylvania and New York USA, Australia, Greenland, England and Denmark (Rasetti, 1948; Robison, 1964; Öpik, 1979; Palmer *et al.*, 1984; Robison, 1994; Weidner and Nielsen, 2014), the *Ptychagnostus atavus* Zone to the *Ptychagnostus punctuosus* Zone of Siberia and Norway (Egorova *et al.*, 1982; Høyberget and Bruton, 2008) and the *Ptychagnostus atavus* Zone to the *Lejopyge laevigata* Zone of Argentina and China (Tortello and Bordonaro, 1997; Peng and Robison, 2000). In the present study *Hypagnostus parvifrons* occurs from the *Peronopsis scutalis* Zone to the *Ptychagnostus*

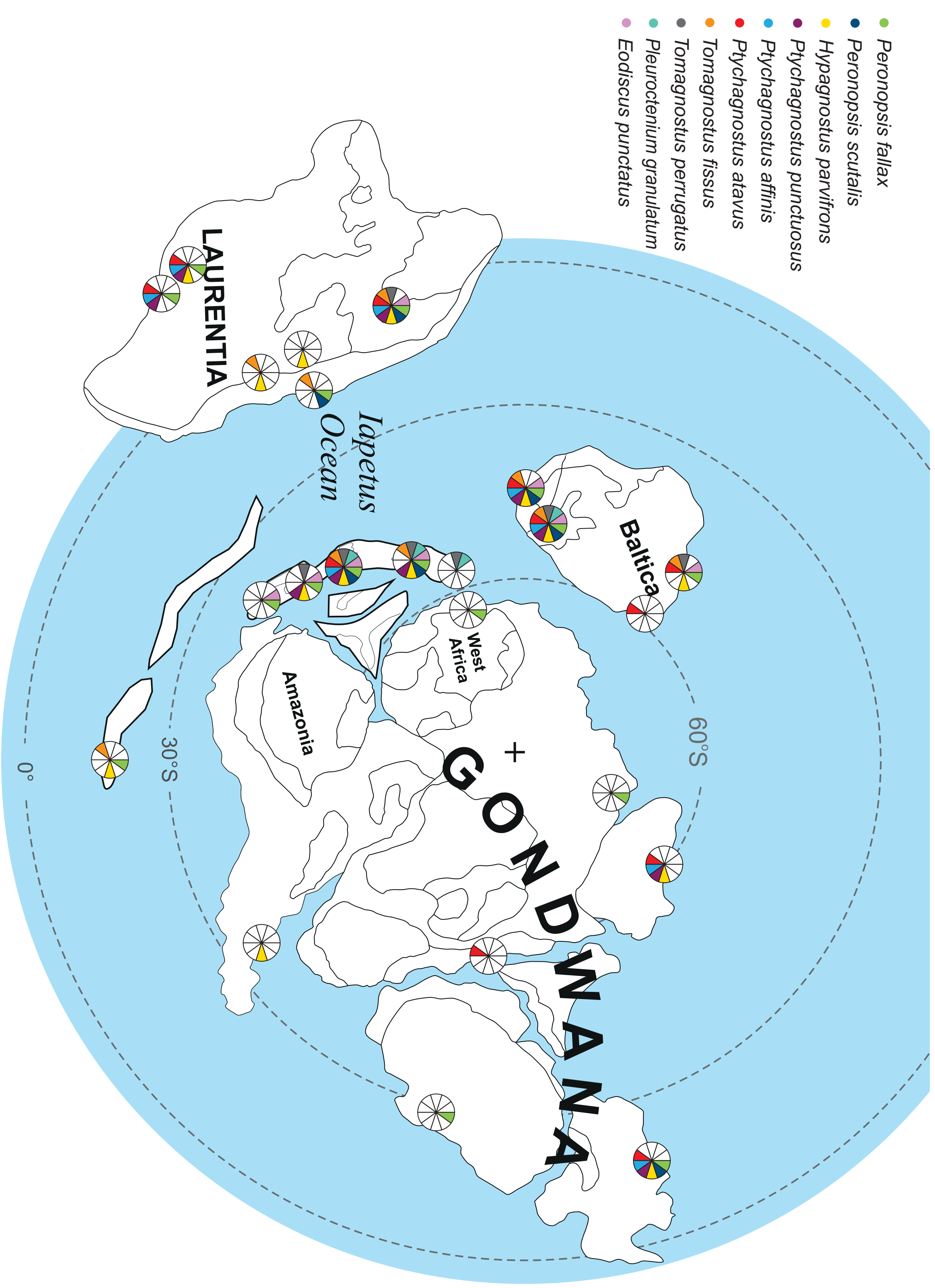

Fig. 30: Middle Cambrian (502 Ma) distribution of agnostoid trilobite species. The palaeogeographic map is based on Pollock *et al.* (2012) and modified from Austermann (2016).

affinis Zone of Eastern Newfoundland.

Ptychagnostus punctuosus (Angelin, 1851) is cosmopolitan and was reported from the middle Cambrian *Ptychagnostus punctuosus* Zone of e.g. New Brunswick, Nevada and Utah (USA), Wales, England, Greenland, Norway, Sweden, Denmark, China and Australia (Illing, 1915; Westergård, 1946; Poulsen, 1969; Öpik, 1979; Allen *et al.*, 1981; Berg-Madsen, 1984; Robison, 1984; Peng and Robison, 2000; Weidner *et al.*, 2004; Høyberget and Bruton, 2008). In the present study *Ptychagnostus punctuosus* occurs in the *Ptychagnostus punctuosus* Zone of Eastern Newfoundland.

Ptychagnostus affinis (Brøgger, 1879) is widespread and was reported from the middle Cambrian *Ptychagnostus atavus* Zone of e.g. China (Peng and Robison, 2000), the upper part of the *Ptychagnostus atavus* Zone of Greenland and Denmark (Robison, 1994; Weidner and Nielsen, 2014) and upper part of the *Ptychagnostus atavus* Zone to the *Ptychagnostus punctuosus* Zone of Nevada and Utah (USA), Sweden, Norway and Australia (Westergård, 1946; Öpik, 1979; Robison, 1984; Høyberget and Bruton, 2008; Weidner and Nielsen, 2009). In the present study *Ptychagnostus affinis* occurs from the lower *Ptychagnostus affinis* Zone of Eastern Newfoundland.

Ptychagnostus atavus (Tullberg, 1880) is widespread and was reported from the middle Cambrian lower part of the *Ptychagnostus atavus* Zone of e.g. Öland, Sweden and Denmark (Weidner and Nielsen, 2009; Weidner and Nielsen, 2014), the *Ptychagnostus atavus* Zone of North America, Norway, Kazakhstan, Siberia, Korea and Australia (Öpik, 1979; Ergaliev, 1980; Egorova *et al.*, 1982; Robison, 1982; Høyberget and Bruton, 2008; Hong and Choi, 2015), the upper part of the *Ptychagnostus atavus* Zone of Greenland (Robison, 1994) and the *Ptychagnostus atavus* Zone to the lower part of the *Ptychagnostus punctuosus* Zone of China (Peng and Robison, 2000). In the present study *Ptychagnostus atavus* occurs from the lower part of the *Ptychagnostus atavus* Zone of Eastern Newfoundland.

Tomagnostus fissus (Lundgren in Linnarsson, 1879) is cosmopolitan and was reported from the middle Cambrian *Ptychagnostus gibbus* Zone to the upper part of the *Ptychagnostus atavus* Zone (Høyberget and Bruton, 2008; Weidner and Nielsen, 2014). In addition, it is reported from the upper part of the *Ptychagnostus gibbus* Zone to the lower part of the *Ptychagnostus atavus* Zone of e.g. Sweden and Greenland (Westergård, 1946; Robison, 1994), the lower part of the *Ptychagnostus atavus* Zone of Denmwark and Siberia (Pegel, 2000; Weidner and Nielsen, 2014) and the *Ptychagnostus atavus* Zone of Massachusetts and South Carolina (USA), Norway, England, Scottland and Western Newfoundland (Kindle, 1982; Illing, 1915; Samson *et al.*, 1990; Høyberget and Bruton, 2008). In the present study *Tomagnostus fissus* occurs from the lower part of the *Tomagnostus fissus* Zone of Eastern Newfoundland.

Tomagnostus perrugatus (Grönwall, 1902) is widespread and was observed from the middle Cambrian *Ptychagnostus gibbus* to the *Ptychagnostus punctuosus* Zone (Rushton, 1979; Robison, 1994). It has been reported of the *Ptychagnostus gibbus* to the *Ptychagnostus atavus* Zone of e.g. England, Sweden and the Czech Republic (Westergård, 1946; Rushton, 1979; Fatka and Kordule, 1992) and the *Ptychagnostus atavus* Zone of Newfoundland, Greenland, Denmark and Siberia (Hutchinson, 1962; Egorova *et al.*, 1982; Robison, 1994; Weidner and Nielsen, 2014). In the present study *Tomagnostus perrugatus* occurs from the *Peronopsis scutalis* Zone to the lower part of the *Ptychagnostus affinis* Zone of Eastern Newfoundland.

Pleuroctenium granulatum (Barrande, 1846) was reported from the middle Cambrian *Ptychagnostus atavus* Zone of e.g. Newfoundland, Wales, England and the Czech Republic (Šnajdr, 1958; Hutchinson, 1962; Smith and White, 1963; Rushton, 1979) and the upper part of the *Ptychagnostus atavus* Zone of Sweden (Westergård, 1946). In the present study *Pleuroctenium granulatum* occurs from the *Peronopsis scutalis* Zone to the *Ptychagnostus affinis* Zone of Eastern Newfoundland.

Eodiscus punctatus (Salter, 1864b) is widespread and was reported from the middle Cambrian lower part of the *Ptychagnostus atavus* Zone of Siberia (Egorova *et al.*, 1982), the *Ptychagnostus atavus* Zone of Nova Scotia and Greenland (Hutchinson, 1952; Poulsen, 1969), the upper part of the *Ptychagnostus atavus* Zone of Wales and England (Matthew, 1886; Illing, 1915), the upper part of the *Ptychagnostus atavus* Zone to the lower part of the *Ptychagnostus punctuosus* Zone of Eastern Newfoundland, Denmark and Sweden (Grönwall, 1902; Westergård, 1946; Hutchinson, 1962; Fletcher, 2006; Weidner and Nielsen, 2014) and the *Ptychagnostus punctuosus* Zone of Norway (Høyberget and Bruton, 2008). In the present study *Eodiscus punctatus* occurs from the *Peronopsis scutalis* Zone to the upper part of the *Ptychagnostus affinis* Zone of Eastern Newfoundland.

The Manuels River fauna shows similarities to middle Cambrian faunas of Canada (West Newoundland, New Brunswick, Nova Scotia and Québec) South England, Wales, the Czech Republic, Spain, Norway, Sweden, Denmark, Turkey, Siberia, Kazakhstan, Greenland, USA (Pennsylvania, Massachusetts, Utah, Nevada and South Carolina), Argentina, Korea, South China, Australia and Antarctica.

6. **Discussion**

The agnostoid bearing beds of the Manuels River Formation are exposed along the west bank of the Manuels River, Newfoundland. The fauna comprises two suborders, four families, six genera and ten species. Similar faunas were reported from other Avalonian localities (e.g., Nova Scotia, New Brunswick, Wales and southern England) and from Baltica (Sweden, Norway, Denmark) (Salter, 1864a,b; Linnarsson, 1869; Tullberg, 1880; Matthew, 1886; Grönwall, 1902; Lake, 1906,1907; Cobbold, 1911; Illing, 1915; Howell, 1925; 1935; Strand, 1929; Westergård, 1946; Hutchinson, 1952, 1962; Rushton, 1966, 1979; Allen *et al.*, 1981; Berg-Madsen, 1984; Martin and Dean, 1988; Weidner *et al.*, 2004; Fletcher, 2006; Høyberget and Bruton, 2008; Weidner and Nielsen, 2009, 2014). In addition, several other Cambrian areas, such as Utah and Nevada (USA), Siberia, Greenland and Australia, show similar faunas (Walcott, 1913; Whitehouse, 1939; Robison, 1964, 1984, 1994; Poulsen, 1969; Öpik, 1979; Egorova *et al.*, 1982; Babcock, 1994; Jago and Bentley, 2010). By contrast, other faunas agree only minor with the herein studied fauna, e.g., from western Newfoundland, Quebec, Pennsylvania, Massachusetts, South Carolina, Spain, the Czech Republic, Turkey, Kazakhstan, Argentina, South Korea and Antarctica (Rasetti, 1948; Palmer and Gatehouse, 1972; Ergaliev, 1980; Gil Cid, 1981; Dean, 1982; Palmer *et al.*, 1984; Samson *et al.*, 1990; Fatka and Kordule, 1992; Westrop *et al.*, 1996; Tortello and Bordonaro, 1997; Hong and Choi, 2015).

Besides the distinct similarities of the faunas, it is remarkable that several other Avalonian, Baltic and Laurentian agnostoid faunas show a higher diversity than the present one (e.g., Westergård, 1946; Robison, 1994; Høyberget and Bruton, 2008). The depositional environment and facies are of particular interest for the comparison of faunas. Different environments, e.g., with respect to water temperature and salinity, may lead to different faunas. The Manuels River Formation was deposited in an oxygen depleted environment (see Austermann, 2016), which also bay have caused the depletion of the fauna. In addition, other studies include larger areas (e.g., Hutchinson, 1962; Peng and Robison, 2000; Høyberget and Bruton, 2008; Weidner and Nielsen, 2014) and/or longer time intervals. As several species occur in more than one biozone, these studies examined a more extend fossil record.

The interval 6.00–6.60 m of the studied succession is devoid of agnostoid trilobites. According to Austermann (2016), the clay mineralogy of this interval show an increase in Fe-chlorite with a simultaneous decrease in kaolinite. This probably indicates a sudden change from relatively warm to relatively cold climate, which may have caused the absence of the agnostids. The interval 11.80–12.10 m of the succession is characterised by a low-diverse agnostid fauna. *Ptychagnostus atavus* occurs abundantly in the interval 11.90–12.06 m and *Tomagnostus perrugatus* sporadically at 11.95 m. In addition, the clay mineralogy of

Austermann (2016), this interval show an increase in kaolinite and a decrease in Fe-chlorite. This difference from the lower part of the succession possibly may indicate a change from temperate to very warm climate. The level 10.76 m is remarkable, as diversity of the fauna switches from low to high. This is possibly caused by a facies change, such as a drop in water level (see Austermann, 2016).

The proposed five agnostoid biozones *Peronopsis scutalis*, *Tomagnostus fissus*, *Ptychagnostus atavus*, *Ptychagnostus affinis* and *Ptychagnostus punctuosus* are local interval zones for the Manules River Formation at Manuels River. The definitions are based on first appearance datums (FADs) of the index species and correlated with the global standard of Peng *et al.* (2012) (see Geyer and Shergold, 2000; Peng and Robison, 2000). The previous, especially in Avalonia common *Hydrocephalus hicksi* and *Paradoxides davidis* zones of Howell (1925), Hutchinson (1962), Landing and Westrop (1998a) and Fletcher (2006) for Avalonia, can be well correlated using Howell's (1925) study. However, a precise correlation is not possible, as the authors either did not sample stratigraphically (e.g., Hutchinson, 1962) or did not provide a detailed systematic work (e.g., Howell, 1925).

Middle Cambrian biozonations have been established for Baltica (e.g., Westergård, 1946; Høyberget and Bruton, 2008; Weidner and Nielsen, 2009, 2014), Siberia (Egorova *et al.*, 1982), South China (Peng and Robison, 2000) and Laurentia (Robison, 1984). The present study agrees in part well with these studies and the global standard. The *Ptychagnostus punctuosus* Zone agrees well with other regions and continents. Correlation with the other zones are not possible, although the *Tomagnostus fissus* Zone of Baltica and Siberia show a similar range to that of the present study. The relative geographic proximity of Avalonia to Baltica, Siberia and Greenland (Laurentia) (Fig. 30) probably explains the similarity in the general agnostoid faunas. A proximity is also supported by the endemism of *Pleuroctenium granulatum*, which is only reported from Avalonia and Baltica (Sweden) (Westergård, 1946; Šnajdr, 1958; Hutchinson, 1962; Rushton, 1979; Fatka *et al.*, 2004; Fletcher, 2006). The Avalonian closly related areas of New Brunswick (Matthew, 1886), Nova Scotia (Hutchinson, 1952), Czech Republic (Šnajdr, 1958; Fatka and Kordule, 1992; Fatka *et al.*, 2004) lack information about agnostoid trilobites, as the areas either have not been the subject of recent studies or the studies did not focus on agnostids. By contrast, the lack of correlation with Laurentia and southern China may indicate a larger distance and/or ocean barriers (Robison, 1984; Peng and Robison, 2000) delaying or preventing the distribution of agnostoid faunas. However, a direct geographic connection of Avalonia and Baltica during the middle Cambrian can be exluded (e.g., McKerrow *et al.*, 1992; Pollock *et al.*, 2012).

The *Ptychagnostus atavus* and *Tomagnostus fissus* zones are proposed to coincide with Howell's (1925) *Hydrocephalus hicksi* Zone, although the boundaries are uncertain (Martin and Dean, 1988). The detailed sampling of the Manuels River Formation carried out in the present study has shown that *Ptychagnostus atavus* occurs only in the interval. Thus, a combined zone of *Tomagnostus fissus* and *Ptychagnostus atavus* can not be justified here. However, the absence of *Ptychagnostus atavus* in the lower part of the formation may be caused by facies fluctuations (see Austermann, 2016). Martin and Dean (1988) collected also from other areas and the exposures at Manuels River might be slightly different. In addition, the origin of some of the material of Martin and Dean (1988) is doubtful (see Chapter *Ptychagnostus punctuosus*). Hutchinson (1962) reported *P. atavus* from the upper level of the *Hydrocephalus hicksi* Zone to the lower level of the *Paradoxides davidis* Zone at Chapel Arm, Trinity Bay, Newfoundland. In addition, it is remarkable that *Ptychagnostus atavus* has not been reported from other areas of Avalonia, except from Manuels River carried out from Hutchinson (1962) and the present study (Fig. 30). However, Geyer and Shergold (2000) listed the species from the United Kingdom, though whithout citations. Also, the species is not recorded from nearby areas such as western Newfoundland and Spain. The Global boundary Stratotype Section and Point (GSSP) for the Drumian Stage, Cambrian Series 3, was designated in the Drum Mountains, Wheeler Formation, Utah, USA (Babcock *et al.*, 2007). The GSSP was selected at the FAD of *Ptychagnostus atavus* because of its cosmoplitan occurrence in comparison to other middle Cambrian agnostoid trilobites after Geyer and Shergold (2000) and Babcock *et al.* (2007).

7. **Conclusions and outlook**

Detailed bed-by-bed sampling of the 19-m-thick Manuels River Formation at the type locality and taxonomic descriptions of agnostoid trilobites is based on 1408 specimens assigned to the suborders Agnostina and Eodiscina, families Peronopsidae, Ptychagnostidae, Condylopygidae and Eodiscidae, genera *Peronopsis*, *Hypagnostus*, *Ptychagnostus*, *Tomagnostus*, *Pleuroctenium* and *Eodiscus* and the species *Peronopsis fallax*, *P. scutalis*, *Hypagnostus parvifrons*, *Ptychagnostus punctuosus*, *P. affinis*, *P. atavus*, *Tomagnostus fissus*, *T. perrugatus*, *Pleuroctenium granulatum* and *Eodiscus punctatus*. The succession comprises five interval biozones, from base to top: *Peronopsis scutalis* Zone, *Tomagnostus fissus* Zone, *Ptychagnostus atavus* Zone, *Ptychagnostus affinis* Zone and *Ptychagnostus punctuosus* Zone. Each zone is characterised by a typical agnostoid assemblage. The *Ptychagnostus punctuosus* Zone can be compared regionally and globally, whereas precise correlations are as yet not possible. The absence of agnostoid trilobites in the interval 6.00–6.60 m is caused by a sudden climate change from relatively warm to relatively cold. By contrast, in the interval 11.90–12.06 m possibly occurred a climate change from temperate to very warm, which caused the occurrence of *Ptychagnostus atavus* in a low diverse assemblage. The species abundance changes from low to high at the stratigraphic level of 10.76 m, caused by a facies change from high-energy to low-energy conditions. The faunal assemblage is comparable to that of Baltica and Greenland, which suggests geographic proximity during the middle Cambrian. *Pleuroctenium granulatum* is endemic to Avalonia and Baltica.

The present study showed the agnostoid trilobite assemblage of the Manuels River Formation at its type locality. For reliable correlation with regional and global biozones, the agnostoid taxonomic descriptions should be supplemented by trilobites of the orders Ptychopariida and Redlichiida, which are in need of revision. Detailed studies of other regions exposing the Manuels River Formation, such as Branch, St. Mary's Bay, Random Island in Newfoundland, St. Pierre and Miquelon, Nova Scotia, New Brunswick and New England, are planned. In addition, older collections, for example, of J. Bergström and T. Fletcher are important for comparisons.

The entire fossil assemblage, including brachiopods and small shelly fossils, is also of interest for the definition of the biozones. Several authors (e.g., Bengtson *et al.*, 1990; Landing *et al.*, 2002; Skovsted and Peel, 2007) emphasized the importance of small shelly fossils for Cambrian biostratigraphy. Hildenbrand (2012) reported on their occurrence in the Manuels River Formation (middle Cambrian) and in southeastern Newfoundland for the first time. This is a promising sign for the occurrence of small shelly faunas in other Avalonian regions.

The Cambrian succession at Manuels River comprises also the upper Cambrian Elliot

Cove formation, which unconformably overlies the Manuels River Formation. The Elliot Cove formation is in need of stratigraphic revision, as the base and the top remain undefined (see Austermann, 2016). Despite the study of Hutchinson (1962), the palaeontology of this formation also needs to be refined and revised.

The present study showed the issues of palaeogeography regarding the palaeontology. Cambrian palaeogeography and climate are still under discussion. Revision of the faunas of Avalonia and adjacent areas will provide new insights into the conditions of the continents during the Cambrian. These research topics will be part of a postdoc project by the present author and co-worker Gregor Austermann, focussing on the sedimentology and palaeontology of the Cambrian basins of West Avalonia and adjacent areas. The project will be fully financed by the Klaus Tschira Foundation (KTS 00.272.2015).

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