BIOSTRATIGRAPHY AND TAXONOMY OF DRUMIAN (MIDDLE CAMBRIAN) AGNOSTID TRILOBITES OF THE MANUELS RIVER FORMATION, AVALONIAN NEWFOUNDLAND, CANADA

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Abstract: New, accurately located and well-preserved agnostid trilobite material has been collected from the type locality of the Drumian (middle Cambrian, Miaolingian) Manuels River Formation, Newfoundland, Canada. The well-exposed grey to black shales containing the fauna were deposited on the former microcontinent Avalonia. Four interval zones for the succession are proposed, namely, the *Tomagnostus fissus*, *Hypagnostus parvifrons*, *Ptychagnostus atavus* and *Ptychagnostus punctuosus* zones. The *Tomagnostus fissus* and *Ptychagnostus atavus* zones are distinct from each other, which leads to a significantly shorter and stratigraphically higher *Ptychagnostus atavus* Zone compared with other sections (Scandinavia, South China, Utah and Nevada, Greenland). Specimens of *Ptychagnostus atavus*, however, occur abundantly, with 107 specimens identified in a short interval of the succession. The *Ptychagnostus punctuosus* Zone can be correlated globally. The faunal assemblage is comparable to that of Scandinavia, Greenland and England. *Ptychagnostus affinis* is recorded for the first time from Avalonia. The 1408 collected specimens were assigned to the suborders Agnostina and Eodiscina and to the families Peronopsidae and Ptychagnostidae, and Condylopygidae and Eodiscidae, respectively, with the following species: *Peronopsis fallax* (Linnarsson), *Peronopsis scutalis* (Hicks), *Hypagnostus parvifrons* (Linnarsson), *Ptychagnostus punctuosus* (Angelin), *Ptychagnostus affinis* (Brøgger), *Ptychagnostus atavus* (Tullberg), *Tomagnostus fissus* (Lundgren), *Tomagnostus perrugatus* (Grönwall), *Pleuroctenium granulatum* (Barrande) and *Eodiscus punctatus* (Salter).

Key words: Cambrian, trilobite, Agnostida, taxonomy, biostratigraphy, Avalonia.

Trilobites of the Order Agnostida are common in Cambrian rocks and are important biostratigraphic tools, given their rapid evolution and wide distribution. They are generally abundant in open-shelf facies from the middle Wuliuan Stage to the end of the Drumian Stage (Geyer & Shergold 2000; Peng & Robison 2000). Because of their abundance and widespread distribution, they also provide data for palaeobiogeographic reconstructions (Høyberget & Bruton 2008; Weidner & Nielsen 2014).

The material for this study was collected from the type locality of the Drumian (middle Cambrian, Miaolingian) Manuels River Formation at Manuels River, Conception Bay South, Avalon Peninsula, Newfoundland (Fig. 1). The formation is also exposed at Trinity Bay, Placentia Bay and the western part of St Mary's Bay, and on the southern Burin Peninsula, Random Island, the French islands of St Pierre and Miquelon, and Cape Breton Island (Nova Scotia). Detailed palaeontological studies of the formation at Manuels River were carried out by Howell (1925) and Hutchinson (1962). Howell (1925) studied the succession in detail, and Hutchinson (1962) provided a lithostratigraphic overview of the Avalon region and systematic descriptions of the trilobite fauna. Subsequent studies on trilobites from the Manuels River Formation have largely focused on polymerids of the orders Ptychopariida and Redlichiida (e.g. Poulsen & Anderson 1975; Bergström & Levi-Setti 1978). Other palaeontological studies deal with microfossils, such as acritarchs (Martin & Dean 1988).

In order to obtain material for a revision and refinement of the systematics and biostratigraphy of agnostid trilobites, specimens were collected bed by bed from the highly fossiliferous shales exposed at the type locality of the formation.
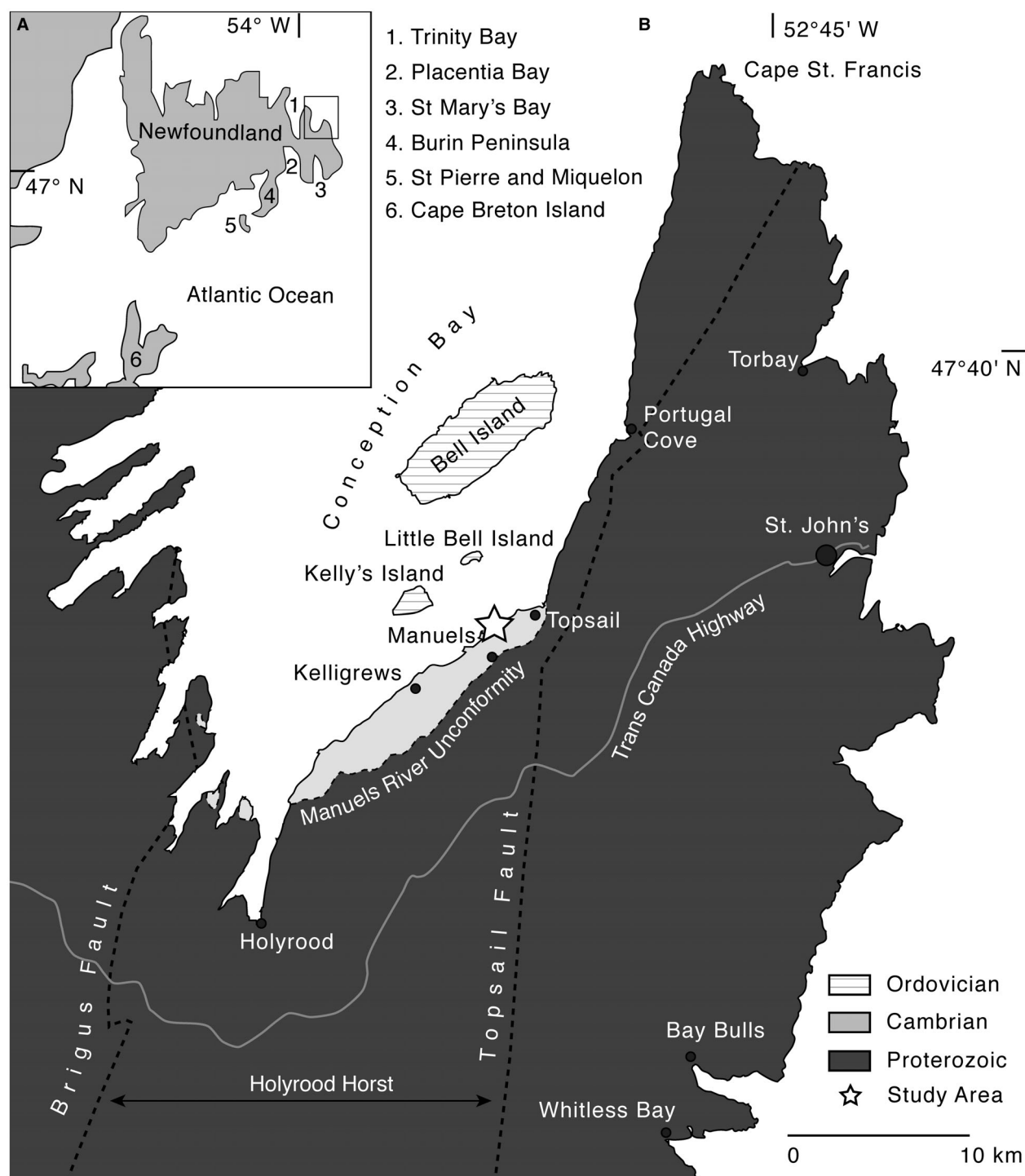
FIG. 1. A, map of Newfoundland. B, expanded view of Conception Bay area, showing the studied outcrop at Manuels River. Kelligrews, Manuels and Topsail are within the city limits of Conception Bay South.

GEOLOGICAL SETTING

In the early Palaeozoic, eastern Newfoundland was part of the microcontinent Avalonia, which is considered to be the largest terrane of the peri-Gondwanan realm (Pollock *et al.* 2012). In the middle Cambrian, Avalonia was connected to Baltica and Gondwana and was located in southern latitudes (Torsvik & Cocks 2017). The general geology of the Avalon Peninsula of Newfoundland has been described and discussed by several authors, for

example Brückner (1978), Anderson (1987), Poulsen & Anderson (1975), King (1990), Boyce (2001) and Fletcher (2006). The type locality of the Manuels River Formation is situated in the valley of the Manuels River, Conception Bay South, Newfoundland (Fig. 1), at 47.525214, −52.951254 (WGS 84). The base of the formation is exposed *c.* 4 m above mean sealevel. The valley, including the outcrop and its fossils, is under government protection by Newfoundland and Labrador law, Regulation 67/11 of the Palaeontological Resource Regulations under the Historic Resources Act.

The Cambrian sedimentary succession exposed along Manuels River (Fig. 1) rests on Neoproterozoic magmatic rocks (e.g. rhyolites, granites and dacites) of the Holyrood Horst (King 1988). The Holyrood Horst represents the basement of the overlying sedimentary rocks and is bordered by two main faults (Topsail and Brigus faults) on the western and eastern margins (Rose 1952; King 1988, 1990) (Fig. 1). On the entire Avalon Peninsula, the Cambrian successions consist of shallow to deep marine sedimentary rocks with only minor faults (Hutchinson 1952, 1962; Fletcher 1972, 2006; Landing 2004).

At Manuels River, the lowermost Cambrian rocks belong to the Brigus Formation (Anderson 1987; Hutchinson 1962), which consists of a basal conglomerate overlain by mudstones with thin intercalations of limestone (Anderson 1987; Landing & Westrop 1998). The top of the formation is truncated by an erosional surface. The base of the disconformably overlying Miaolingian Chamberlain's Brook Formation consists of a manganese bed overlain by greenish mudstones. The boundary between the Chamberlain's Brook Formation and the conformably overlying Manuels River Formation is marked by a thin volcanic ash layer. Howell (1925) established the Chamberlin's Brook Formation (his beds 1–35), Long Pond Formation (his beds 36–92), and Kelligrew Brook Formation (his beds 93–125) for the strata along Manuels River. Subsequently, Hutchinson (1962) renamed and defined the Chamberlin's Brook Formation as Chamberlain's Brook Formation and merged Howell's (1925) Long Pond and Kelligrew Brook formations (beds 36–125) into his Manuels River Formation, composed mainly of black shales with interbedded thin volcanic ash layers and carbonate concretions (Austermann 2016). The contact with the overlying, not yet formally defined Elliot Cove formation, is unconformable and is marked by a coarse sandstone/conglomerate (Howell 1925, bed 125; Hutchinson 1962; Poulsen & Anderson 1975; Austermann 2016).

MATERIAL AND METHOD

A total of 1408 specimens have been collected from the type locality. All specimens are stored at The Rooms Corporation of Newfoundland and Labrador, Provincial Museum Division, Natural History Unit, St John's, Newfoundland, Canada. Currently, the agnostid collection of Manuels River is on loan to Heidelberg University, Heidelberg, Germany. The herein studied collection has been supplemented with type specimens from the collections of Hutchinson (1962) and Martin & Dean (1988), with their collections housed in the Geological Survey of Canada, Ottawa, Canada.

Agnostid classification and terminology follow that of Shergold *et al.* (1990), Whittington *et al.* (1997), Peng & Robison (2000) and Robison (1982).

Matthews (1973), Bengtson (1988) and Becker (2001) are followed for abbreviations and symbols used for detailed nomenclatural decisions and statements. The specimens were photographed and measured with a Keyence VHX-6000 digital microscope with integrated LED light from the upper left. The illustrated photographs were calibrated with Adobe Illustrator CC.

BIOSTRATIGRAPHY

Local biostratigraphy

The first biostratigraphic zonation of the Manuels River Formation was established by Howell (1925). Before Howell's work, authors focused on the subdivision of the entire Conception Bay area, and the North American continent in general, rather than on detailed biostratigraphy (Murray 1869; Murray & Howley 1881; Matthew 1886, 1896, 1899; Walcott 1888*a*, *b*, 1889, 1891, 1900; Marcou 1890). Howell (1925) described the black shale successions along the Manuels River in detail and established three trilobite-based biozones, the *Paradoxides bennetti* Zone (Howell's beds 1–35), the *Paradoxides hicksi* Zone (beds 36–92), and the *Paradoxides davidis* Zone (beds 93–125), the latter two zones corresponding to the present Manuels River Formation. The distribution of agnostid trilobites and species of the orders Ptychopariida and Redlichiida were documented.

Howell's (1925) fossil collections were deposited in different museums, the last identifiable location being the Smithsonian National Museum of Natural History, Washington DC, USA, where some of the type specimens are housed. The major part of Howell's material has not been found there or anywhere else and must be considered lost. Hutchinson (1962) confirmed the local biostratigraphic zones of Howell's (1925) beds 36–125 and introduced the name Manuels River Formation for this succession. He revised and supplemented the work of Howell, especially the systematics of the agnostid trilobites. His detailed work includes numerous descriptions and illustrations. Poulsen & Anderson (1975) subdivided

the succession corresponding to the upper Manuels River Formation and the lower Elliot Cove formation biostratigraphically using Scandinavian trilobite zones, which are based on trilobites of different orders, including agnostids. They identified *Ptychagnostus punctuosus* (Angelin, 1851) in the *Ptychagnostus punctuosus* Zone from the Highland Cove assemblage, south-eastern Newfoundland (corresponding to the upper part of the *Paradoxides davidis* Zone of Hutchinson 1962). For global correlation of this upper middle Cambrian zone, see the section '*Ptychagnostus punctuosus*'. Bergström & Levi-Setti (1978) studied the upper part of the Manuels River Formation bed by bed on the north-eastern banks of the river. They described two subspecies of *Paradoxides davidis* Salter, 1863 (*Pa. davidis trapezopyge* and *Pa. davidis intermedius*) from different intervals of the formation, but no agnostids were reported. The authors followed the concept of the *Pa. davidis* Zone of Howell (1925) and Hutchinson (1962). Martin & Dean (1981, 1988) studied for the first time acritarchs and trilobites and integrated the biozonations of these groups for the Manuels River succession. They redefined the existing biozones and established three trilobite biozones, namely, the *Tomagnostus fissus–Ptychagnostus atavus* Zone, the *Hypagnostus parvifrons* Zone (although with uncertain lower and upper boundaries) and the *Ptychagnostus punctuosus* Zone. The conglomerate of Howell's (1925) bed 125 was taken as the basal bed of the Elliot Cove formation, a concept followed here.

Results and correlation

The mostly cosmopolitan distribution of agnostid trilobites in open-marine sediments, their relatively short stratigraphic ranges and abundant occurrence make them appropriate index fossils (Robison 1984, 1994; Peng & Robison 2000). The interval zone concept is a common tool for chronostratigraphic correlation, in which each agnostid biozone is defined as the interval between the lowest stratigraphic occurrence ('first occurrence', FO) of its eponymous agnostid species and the lowest occurrence of the next selected agnostid species (e.g. Robison 1984; Peng & Robison 2000; Høyberget & Bruton 2008; Weidner & Nielsen 2014). The defining species are selected on the basis of their cosmopolitan distribution, abundance, and their relatively short stratigraphic range (Robison 1984; Peng & Robison 2000). However, the use of FOs for global chronocorrelation suffers from the inherent diachroneity of the species, the magnitude of which varies between species. Precise correlation is possible only in combination with studies of sedimentology and calibration with other zonations (Landing *et al.* 2013). Several studies (e.g. Howell 1925; Westergård 1946; Westrop *et al.* 1996) based on agnostid and/or polymerid trilobites

lack precise definitions of zonal boundaries or used different, non-reproducible descriptive methods, for dividing biozones, as also remarked by Peng & Robison (2000) and Høyberget & Bruton (2008).

Illing (1915) did not define his biozones but described *Paradoxides hicksi* from his *Paradoxides aurora* Zone, which is stratigraphically lower than the *Pa. hicksi* Zone. *Paradoxides hicksi* is rare in both zones and becomes abundant only in the upper part of the *Pa. hicksi* Zone and does not occur at the base of its Zone (divided into a lower and an upper part), but in the uppermost part of the *Pa. davidis* Zone. Given that the biozones are not reproducible, the given range chart allows only a rough correlation. Rushton (1979) adopted Illing's (1915) biozones with minor supplements, although without precise definition. Howell (1925) and Hutchinson (1952, 1962) described their biozones in combination with lithostratigraphy. Given that Howell (1925) described the strata in more detail, Hutchinson (1962) often used Howell's work as a base for his biozones, although without definitions of the zones. The range charts of the described taxa by Howell (1925) and Hutchinson (1962) allow for correlation. According to Westergård (1946), *Hypagnostus parvifrons* occurs in his lower *T. fissus* and *Pt. atavus* Zone (Berg-Madsen 1984; Peng & Robison 2000). Here, we follow the concept of Peng & Robison (2000) to combine Westergård's (1946) *Tomagnostus fissus–Ptychagnostus atavus* and *Hypagnostus parvifrons* zones. As Illing (1915), Hutchinson (1952, 1962), Fletcher (1972, 2006), Rushton (1979), and Landing & Westrop (1998) used polymerid trilobites for their biozones, the integration of Howell's (1925) high-resolution range chart and the range chart of the present study allows for correlation of our biozonation with those of these authors.

Only a few studies provide clear and exhaustive definitions of local biozones (Fletcher 1972, 2006; Robison 1984, 1994; Peng & Robison 2000; Weidner & Nielsen 2014). Here we revise and complement the faunal assemblage and the local biozones of previous studies (e.g. Howell 1925; Hutchinson 1962; Martin & Dean 1988) and correlate the biozones of the Manuels River Formation at Conception Bay globally.

The four local interval zones proposed here are primarily correlated with East and West Avalonia (Newfoundland, Nova Scotia, England), supplemented with Baltica (Scandinavia), Siberia, Laurentia (Utah, Nevada, Greenland) and South China (Figs 2, 3). In the work by Howell (1925) on the type locality of the Manuels River Formation, the *Paradoxides hicksi* and *Pa. davidis* biozones were defined on the basis of the trilobites of the Order Redlichiida, whereas biozones proposed here are based on the Agnostida. We propose the following local biozones for the type locality of the Manuels River Formation.
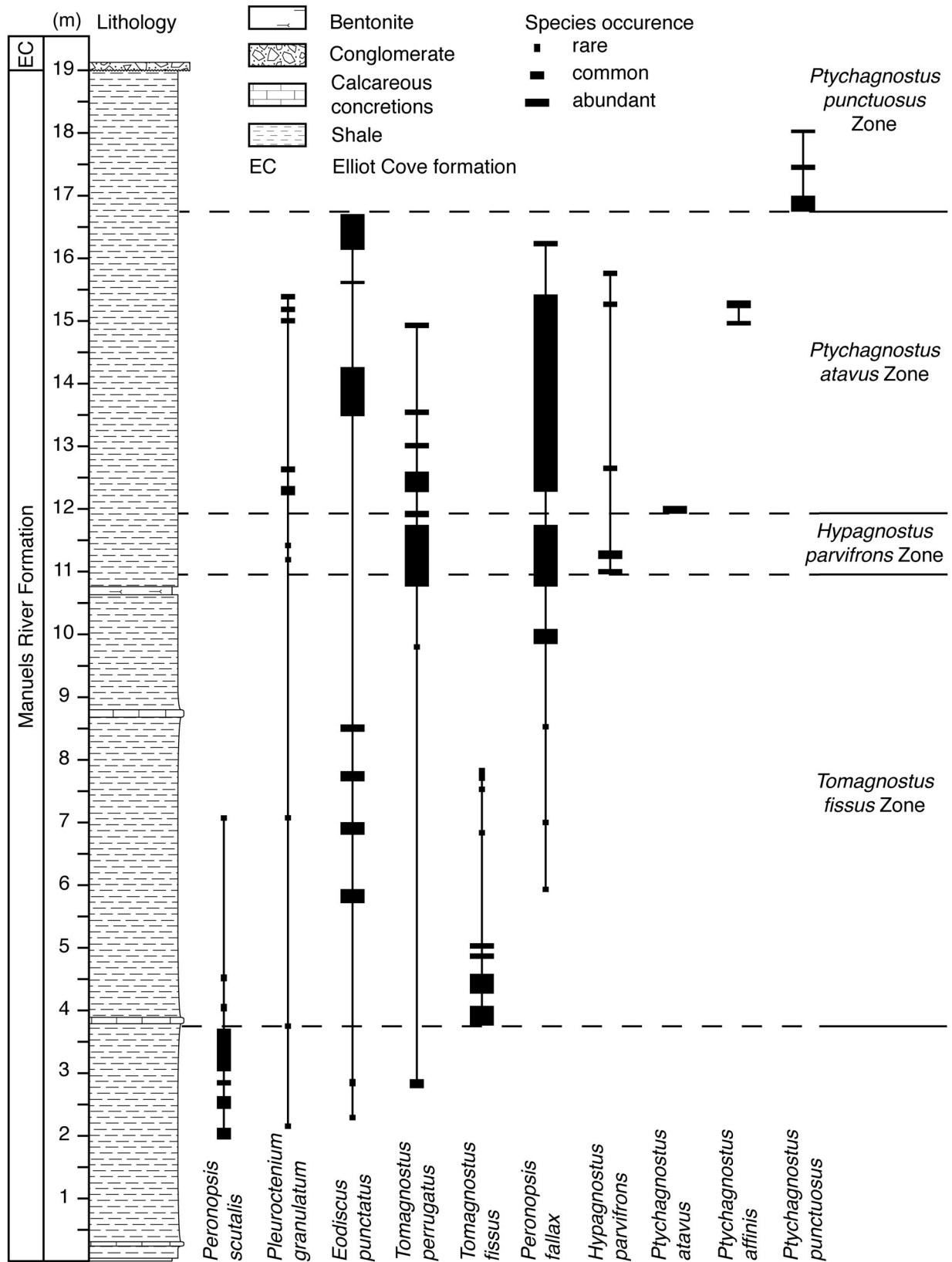
FIG. 2. Stratigraphic distribution and biozonation of agnostid species of the middle Cambrian Manuels River Formation at its type locality along Manuels River, Newfoundland.

Newfoundland			Nova Scotia	England	Scandinavia		Siberia	South China	Utah and Nevada, Greenland
Manuels River	Deep Cove	Highland Cove							
Ptychagnostus punctuosus					*Ptychagnostus punctuosus*			*Ptychagnostus punctuosus*	*Ptychagnostus punctuosus*
Ptychagnostus atavus	*Paradoxides davidis*	*Paradoxides davidis*	*Paradoxides davidis*	*Paradoxides davidis*	*Hypagnostus parvifrons*	*Ptychagnostuts atavus*[1] / *Acidusus atavus*[2]	agnostid zone(s) not named	*Ptychagnostus atavus*	*Ptychagnostus atavus*
Hypagnostus parvifrons									
Tomagnostus fissus	*Paradoxides hicksii*	*Hydrocephalus hicksi*	*Paradoxides hicksi*	*Paradoxides hicksii*	*Tomagnostus fissus and Ptychagnostus (Ptychagnostus) atavus*		*Tomagnostus fissus*		

FIG. 3. Global correlation of the middle Cambrian of Newfoundland, Avalonia. Data sources: Deep Cove: Fletcher 1972, 2006; Highland Cove: Hutchinson 1962; Landing & Westrop 1998; Nova Scotia: Hutchinson 1952; England: Illing 1915; Rushton 1979; Scandinavia: left column, Westergård 1946; right column, (1) Høyberget & Bruton 2008, (2) Weidner & Nielsen 2014; Siberia: Egorova *et al.* 1982; Pegel 2000; South China: Peng & Robison 2000; Utah, Nevada, USA and Greenland: Robison 1984, 1994.

Tomagnostus fissus Zone. The base of the zone is defined by the FO of *T. fissus* at 3.89 m above the base of the Manuels River Formation (Fig. 2). The species ranges up to 7.70 m in section. Co-occurring species at the base of this zone are *Peronopsis scutalis*, *Eodiscus punctatus*, *Pleuroctenium granulatum* and *Tomagnostus perrugatus*. The top of the zone is defined by the FO of *Hypagnostus parvifrons* at the level of 10.96 m.

Hypagnostus parvifrons Zone. The base of the zone is defined by the FO of *H. parvifrons* at 10.96 m above the base of the formation (Fig. 2). *Hypagnostus parvifrons*

ranges well into the overlying *Pt. atavus* Zone. The associated assemblage consists of *Peronopsis fallax*, *T. perrugatus* and *Pl. granulatum*. *Eodiscus punctatus* has not been found in the zone, although it occurs in the underlying and overlying zones. The top of the zone is defined by the FO of *Ptychagnostus atavus* at 11.90 m.

Ptychagnostus atavus Zone. The base of the zone is defined by the FO of *Pt. atavus* at 11.90 m above the base of the formation (Fig. 2). The species occurs abundantly up to 12.08 m. Additional species at the base of the zone are *T. perrugatus*, *Pe. fallax*, *Pl. granulatum*, *H. parvifrons* and *E. punctatus*. The top of the zone is defined by the FO of *Pt. punctuosus* at the level of 16.76 m.

Ptychagnostus punctuosus Zone. The base of the zone is defined by the FO of *Pt. punctuosus* at 16.76 m above the base of the formation (Fig. 2). The species ranges up to 18.06 m. There are no other characterizing agnostid species in the *Pt. punctuosus* Zone. The top of the zone cannot be defined at present, because the FO of a suitable species may occur in the overlying Elliot Cove formation, which has not been studied here.

DISCUSSION

Tomagnostus fissus Zone

The *T. fissus* Zone is here established as a local biozone. Howell (1925) proposed the *Paradoxides hicksi* Zone for his beds 36–92, and Hutchinson (1962) followed this suggestion. Nevertheless, our *T. fissus* Zone can be correlated with Howell's *Pa. hicksi* Zone thanks to the precise work of Howell (1925), despite the lack of systematic work on and illustrations of the species. *Peronopsis scutalis* and *Tomagnostus perrugatus* are missing from the faunal assemblage of Howell (1925). Howell reported and Hutchinson (1962) described *Hypagnostus parvifrons* from the *Pa. hicksi* Zone, a species we have found only at a stratigraphically higher level. Hutchinson (1962) described *T. fissus* as the most common agnostid in the *Pa. hicksi* Zone of the Manuels River section. *Ptychagnostus atavus* was described by Hutchinson (1962) from the upper part of the *Pa. hicksi* Zone and the basal *Paradoxides davidis* Zone. Martin & Dean (1988) combined the agnostid occurrences to a *T. fissus–Pt. atavus* Zone, approximately corresponding to the *Pa. hicksi* Zone of Howell (1925). However, they did not describe or report *T. fissus* or *Pt. atavus* from the Manuels River section.

Interregional correlation is possible with the *T. fissus–Pt. atavus* Zone of Baltica (Westergård 1946) and *T. fissus* Zone of Siberia (Egorova *et al.* 1982). *Tomagnostus fissus* is common in the middle Cambrian successions

of Avalonia, Baltica and eastern Laurentia. The species has not been reported from Gondwana, which makes the establishment of a globally working biozone difficult.

Hypagnostus parvifrons Zone

Howell (1925) proposed the *Pa. davidis* Zone for his beds 93–125, which was followed by Hutchinson (1962). Based on a comparison with contemporaneous Scandinavian strata, Martin & Dean (1988) proposed the interval as belonging to the *H. parvifrons* Zone, although with uncertain lower boundary. The dashed line of the boundary is placed in the interval of beds 94–99 of Howell (1925) (10.65–11.30 m), which is close to the FO of *H. parvifrons* at the level of 10.96 m.

The zone correlates with the *H. parvifrons* Zone of Sweden, as defined by Westergård (1946). The associated agnostid assemblage of *Peronopsis fallax*, *T. perrugatus* and *Peuroctenium granulatum* is similar to that in Sweden. Westergård (1946) also described *Pt. affinis* from the *H. parvifrons* Zone, a species that in the Manuels River succession appears only in the overlying *Pt. atavus* Zone.

Although *H. parvifrons* is a widely distributed species, its stratigraphic range varies significantly between regions. Also, the FOs of *H. parvifrons* and *Pt. atavus* occur at close stratigraphic levels, for example in China, Siberia and USA (Peng & Robison 2000). Therefore, the *H. parvifrons* Zone described here should be taken as a local biozone.

Ptychagnostus atavus Zone

The *Pt. atavus* Zone is part of the *Pa. davidis* Zone proposed by Howell (1925) for his beds 93–125, and later adopted by Hutchinson (1962). For beds 99–114, Howell (1925) described the same faunal assemblage as here except for the species *Pt. atavus* and *Pt. affinis*. Detailed sampling for the present study has shown that *Pt. atavus* occurs only in the narrow interval of 11.90–12.08 m, here with 107 specimens. Hutchinson (1962) and Fletcher (2006) reported *Pt. atavus* from the upper *Hydrocephalus hicksi* Zone to the lower *Pa. davidis* Zone from Highland Cove and Cape St Mary's, respectively. Westrop *et al.* (1996) reported *Pt. atavus* from western (Laurentian) Newfoundland. It is remarkable that *Pt. atavus* has not been reported from other areas of Avalonia, for example England, Wales, New Brunswick or Nova Scotia (Matthew 1886; Illing 1915; Hutchinson 1952, 1962; Fletcher 2006; Rees *et al.* 2014). *Ptychagnostus affinis* is reported for the first time from the succession at the Manuels River, and hence also for the entire microcontinent Avalonia.

Ptychagnostus atavus and *Pt. affinis* occur in a very short stratigraphic interval at the type locality, shorter than in other areas in eastern Newfoundland and than in most of the other global occurrences. However, Fletcher (1972, 2006) has shown that the Manuels River Formation is condensed at its type locality compared with other areas in eastern Newfoundland.

The GSSP for the Drumian Stage, Cambrian Series 3, was defined in the Wheeler Formation, Drum Mountains, Utah, USA (Babcock *et al.* 2007). The level was selected at the FO of *Pt. atavus* in the section on the basis of its cosmopolitan occurrence compared with other middle Cambrian agnostid trilobites, such as *H. parvifrons* or *T. fissus* (Geyer & Shergold 2000; Peng & Robison 2000; Babcock *et al.* 2007).

Ptychagnostus punctuosus *Zone*

Ptychagnostus punctuosus is widespread globally and its zone is easy to correlate. Howell (1925) described rare occurrences of *Eodicsus punctatus* (bed 115) and *Pe. fallax* (beds 114–116) besides *Pt. punctuosus*. These beds correspond to the base of the *Pt. punctuosus* Zone proposed here.

CONCLUSIONS

1. The following agnostid species are reported from the type locality of the Manuels River Formation: *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, 1864).
2. The faunal assemblage is comparable to that of Scandinavia, Greenland and England.
3. We propose four local interval zones for the succession, viz. the *Tomagnostus fissus*, *Hypagnostus parvifrons*, *Ptychagnostus atavus* and *Ptychagnostus punctuosus* zones.
4. The *Ptychagnostus punctuosus* Zone can be correlated globally. The remaining biozones are referred to as local.
5. *Ptychagnostus atavus* occurs abundantly (107 specimens) in the interval 11.90–12.08 m. This is a significantly shorter and higher stratigraphic range than in other sections from the *Pt. atavus* Zone (Scandinavia, South China, Utah and Nevada, Greenland).

6. *Ptychagnostus affinis* occurs abundantly (99 specimens) in the interval 14.92–15.32 m and has not previously been recorded from Newfoundland or Avalonia (e.g. Nova Scotia, New Brunswick and England).

Institutional abbreviations. AR, Swedish Museum of Natural History, Stockholm, Sweden; BMNH, Natural History Museum, London, UK (now NHMUK); GSC, Geological Survey of Canada, Ottawa, Canada; LO, Department of Geology, University of Lund, Sweden; MGUH, Geological Museum, University of Copenhagen, Denmark; NFM, Rooms Corporation of Newfoundland and Labrador, Provincial Museum Division, Natural History Unit, St John's, Newfoundland, Canada; NMP, National Museum, Prague, Czech Republic; PMO, Paleontologisk Museum University of Oslo, Norway; SGU, Geological Survey of Sweden, Uppsala, Sweden; SMA, Sedgwick Museum, University of Cambridge, UK.

SYSTEMATIC PALAEONTOLOGY

Superfamily AGNOSTOIDEA M'Coy, 1849
Family PERONOPSIDAE Westergård, 1936

Genus PERONOPSIS Hawle & Corda, 1847

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

Diagnosis. Cephalon non-scrobiculate and smooth; median preglabellar furrow absent; subquadrate to semiovate anterior glabellar lobe; F3 furrow straight; axial node on posterior glabellar lobe near F2 furrow; pygidial axis with F1 and F2 furrows weak to absent; axis with weakly developed transverse depression at midlength (based on Robison 1994; Shergold & Laurie 1997, with modifications).

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

Remarks. *Peronopsis* includes the geologically oldest agnostids of the middle Cambrian (Laurie 1990; Naimark 2012). More than 100 species have been assigned to this genus (Rushton 1979; Robison 1994, 1995; Weidner & Nielsen 2014). The morphological characters vary during ontogeny and within population, which led to a complex taxonomic subdivision of *Peronopsis* (Robison 1982; Naimark 2012). This is why there are frequent discussions about synonyms. *Acadagnostus* Kobayashi, 1939, is a frequently discussed synonym (e.g. Rushton 1979; Laurie 1990; Robison 1994, 1995; Shergold & Laurie 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. In contrast, *Peronopsis* is very variable in the pygidial median postaxial furrow as well as in the occurrence of spines. Shergold & Laurie (1997) presented a diagnosis of *Acadagnostus* in which the pygidial spines and the pygidial axis never reach 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, therefore *Acadagnostus* is here excluded from *Peronopsis*. Some species of *Euagnostus* Whitehouse, 1936 have a median preglabellar furrow, which is not observed in *Peronopsis*. Therefore, Høyberget & Bruton (2008) suggested to exclude this genus from the synonymy list of *Peronopsis*, a view followed here.

Peronopsis fallax (Linnarsson, 1869)
Figures 4, 5

1869 *Agnostus fallax* Linnarsson, pp. 81–82, pl. 2, figs 54–55.

1879 *Agnostus fallax*, Linrs.; Brøgger, pp. 64–65 (pars), pl. 6, fig. 1 (non fig. 1a).

? 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.

1886 *Agnostus acadicus*, Hartt; Matthew, p. 70 (pars), pl. 7, fig. 5a (non fig. 5b).

1886 *Agnostus vir* Matthew, pp. 69–70, pl. 7, fig. 3.

1886 *Agnostus vir*, var. *concinnus* Matthew, p. 70, pl. 7, figs 4a–c.

1892 *Agnostus vir* Matthew; Vogdes, pp. 388–389, pl. 10, fig. 14.

1892 *Agnostus vir* var. *concinnus* Matthew; Vogdes, p. 389, pl 9, fig. 13.

1896 *Agnostus fallax* Linrs.; Matthew, pp. 214–215 (pars), pl. 15, fig. 8a (non fig. 8b).

1896 *Agnostus fallax* var. *vir* Matthew, pp. 215–216, pl. 15, fig. 6.

? 1896 *Agnostus fallax* var. *concinnus* Matthew, p. 216, pl. 15, figs 7a–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 7a–8b; pl. 5, figs 8–9.

1910 *Agnostus acadicus* Hartt; Grabau & Shimer, p. 256 (pars), fig. 1543a (non fig. 1543b).

1911 *Agnostus fallax* Linnarsson; Cobbold, p. 291, pl. 25, figs 17a–18b.

1915 *Agnostus fallax* Linnarsson; Illing, p. 416, pl. 31, figs 12–15.

1925 *Agnostus clarae* Howell, pp. 74–75, pl. 3, fig. 1.

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

1936 *Peronopsis fallax* (Linnarsson); Westergård, pp. 28–29, pl. 1, figs 9–15.

1946 *Peronopsis fallax* (Linnarsson); 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); Henningsmoen, p. 15, pl. 2, fig. 5.

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

1961 *Peronopsis* cf. *fallax* (Linnarsson); 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 & 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; Rushton, p. 50, fig. 3B.

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

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

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

1982 *Peronopsis fallax* (Linnarsson); Egorova *et al.*, pp. 66–67 (pars), pl. 2, fig. 1; pl. 5, fig. 6; pl. 9, figs 3–4; (non pl. 10, fig. 3); pl. 13, fig. 6; pl. 18, fig. 7; pl. 19, fig. 3; pl. 41, figs 3–5, 11; pl. 51, figs 15–16 (non pl. 62, figs 5–6).

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

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

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

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

1990 *Peronopsis fallax* (Linnarsson); Samson *et al.*, p. 1466 (pars), fig. 5A (non fig. 5B).

1994 *Peronopsis fallax* (Linnarsson); Robison, pp. 43–44, figs 19.3–4.

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

1995 *Peronopsis acadica* Hartt (*in* Dawson); Robison, pp. 302–305, figs 1.1–3.

1997 *Acadagnostus fallax* (Linnarsson); Shergold & Laurie, p. 363, figs 230.8a–b.

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

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

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

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

2014 *Acadagnostus acadicus* (Hartt *in* Dawson); Weidner & Nielsen, pp. 60–61, figs 32A–C.

2015 *Peronopsis fallax* (Linnarsson; also identified as *Axagnostus fallax*; see Laurie 1990); Maletz & Steiner, p. 1089, figs 14E, I.
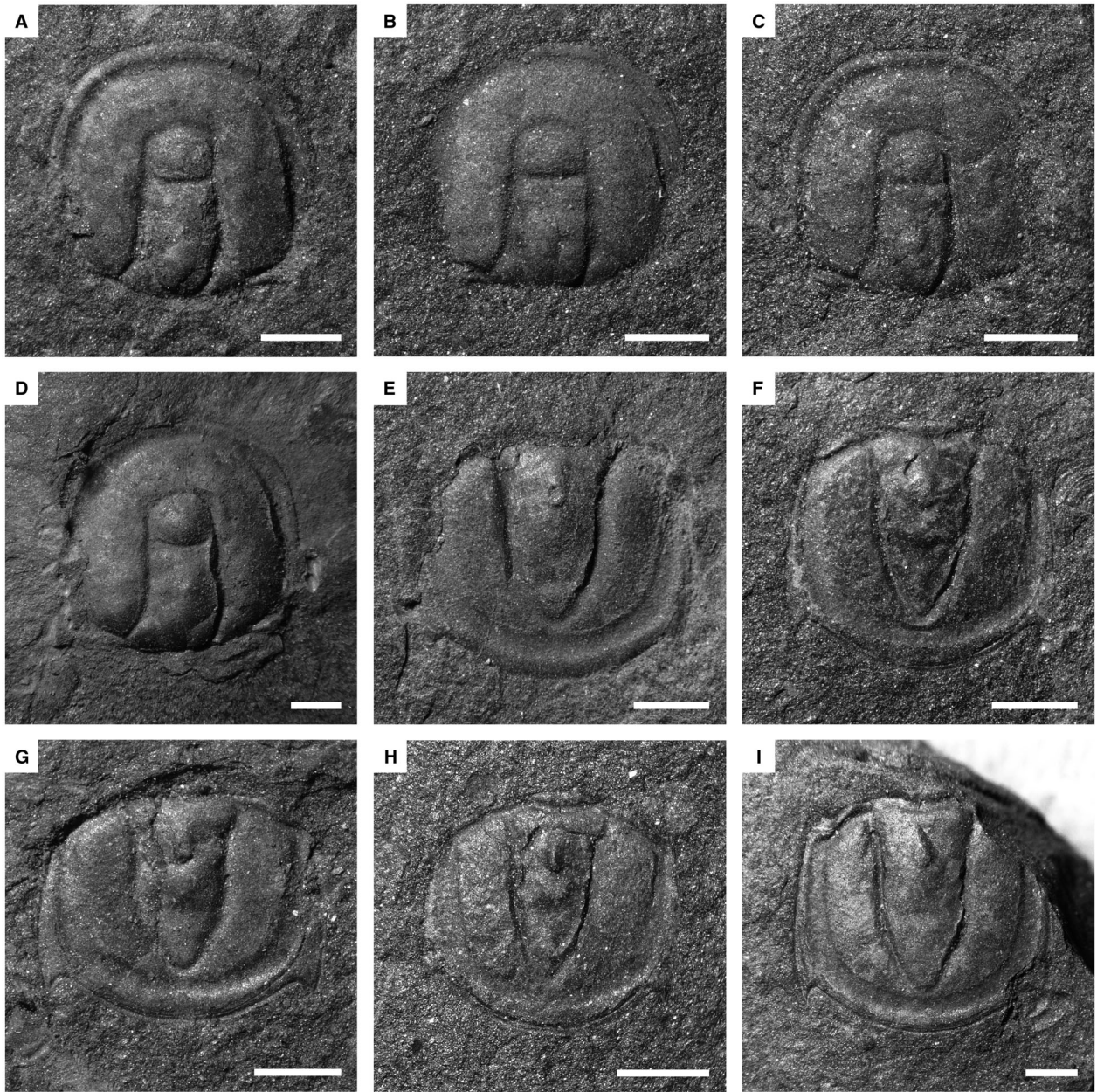
FIG. 4. *Peronopsis fallax* (Linnarsson, 1869). A, cephalon (NFM F-1120). B, cephalon (NFM F-1097). C, cephalon (NFM F-1187). D, cephalon (NFM F-999). E, pygidium (NFM F-1000). F, pygidium (NFM F-1129). G, pygidium (NFM F-1192). H, pygidium (NFM F-1186). I, pygidium (NFM F-1198). Scale bars represent 1 mm.

Lectotype. SGU 4716, by subsequent designation of Laurie (1990, p. 320, fig. 1B), originally figured by Westergård (1946).

Material. 5 complete specimens, 141 cephala and 131 pygidia (NFM F-998–F-1274) from the middle part of the Manuels River Formation type locality (5.91–16.27 m), Conception Bay South, Newfoundland, Canada.

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

Description. The specimens are mainly well-preserved, with complete specimens varying from 3.5 to 7.2 mm in length. The cephala vary in size from 2.4 to 4.9 mm in width and from 2.2 to 4.5 mm in length, and the pygidia vary in size from 1.6 to 5.3 mm in width and from 1.2 to 4.8 mm in length. Some of the specimens show a yellow colour from the pyrite contained
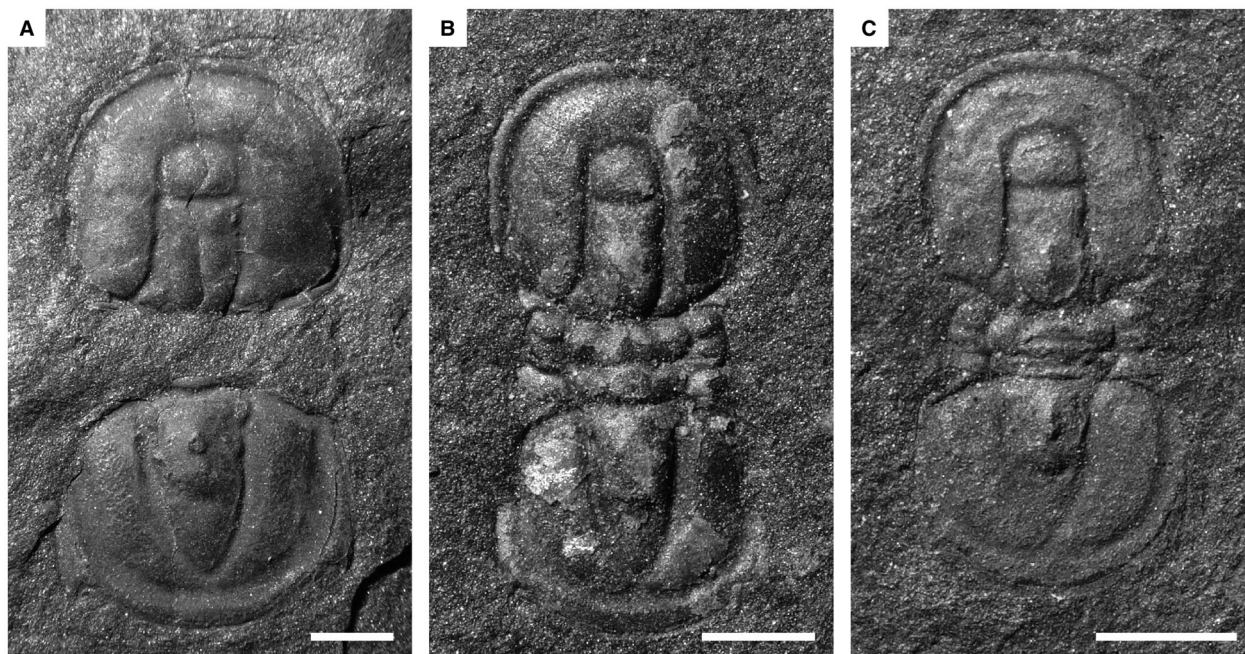
FIG. 5. *Peronopsis fallax* (Linnarsson, 1869). A, complete specimen (NFM F-998). B, complete specimen (NFM F-1064). C, complete specimen (NFM F-1121). Scale bars represent 1 mm.

in the shales. All cephala and pygidia are subquadrate to subcircular, and 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 due to the axis varying in broadness and in the form of the posterior end. 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 visible in some specimens. Some pygidia show a weakly transverse depression at the midlength of the axis. All pygidia show a pair of posterolateral spines.

Remarks. *Peronopsis fallax* is a long-ranging species with a high variability in morphology (Robison 1982; Høyberget & Bruton 2008). The cephala are subquadrate to subcircular. The relative width of the cephala and pygidia increases during ontogeny. This is, for example, visible in characters such as border furrows, which become wider from meraspis to holaspis stage (Robison 1995). The length of the pygidial axis varies, from ending in the postaxial area near the border furrow, to contacting the median postaxial furrow, or reaching the border furrow. Høyberget & Bruton (2008) explained this variation in association with the stratigraphic occurrence of the species and with intraspecies variations. In stratigraphically older specimens, from the early middle Cambrian, the pygidial axis reaches the border furrow, while in later occurring specimens (*Pt. atavus* Zone) the pygidial axis contacts the median postaxial furrow. In addition, the median postaxial furrow weakens or vanishes during advanced ontogeny (Robison 1982). Due to these variations the systematic position of *Pe. fallax* is still controversial (e.g. Hutchinson 1952; Gil Cid

1981; Laurie 1990; Robison 1994, 1995; Høyberget & Bruton 2008; Weidner & Nielsen 2009, 2014).

Robison (1995) and Weidner & Nielsen (2014) considered *Pe. fallax* as a junior subjective synonym of *Agnostus acadicus* Hartt *in* Dawson, 1868). Robison (1995) noted that the type material must be viewed critically, because Hartt (*in* Dawson 1868) was uncertain about the true association of the cephalon and pygidium. Öpik (1979) and Robison (1995) suggested that the questionable type pygidium of Hartt be assigned to *H. parvifrons* (Linnarsson, 1869) (see the *H. parvifrons* section). The illustrated specimen in Dawson (1868) shows a spineless pygidium, which is not characteristic for *Pe. 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 *Ag. acadicus* with pygidial spines instead of non-spinose pygidia. The cephalon sampled by Hartt (*in* Dawson 1868) is in Robison's (1995) view still the holotype of *Ag. acadicus* and therefore a senior subjective synonym of *Pe. fallax*. It is now the type species of *Acadagnostus* Kobayashi, 1939, as described in Shergold & Laurie (1997) (see the *Peronopsis* section). The present study follows the suggestion of Høyberget & Bruton (2008), that Hartt's species should be regarded as a *nomen dubium* because the type material is to be seen as doubtful and is not reviewable.

Peronopsis fallax is distinguished from the closely related species *Peronopsis ferox* (Tullberg, 1880) mainly by characteristics of the pygidia. *Peronopsis ferox* has a broader and shorter pygidial axis than *Pe. fallax*, thus the postaxial area is wider and a median postaxial furrow is absent. In addition, *Pe. ferox* often has a crescent-shaped border between the pair of pygidial posterolateral spines, whereas *Pe. fallax* developed a narrow border of constant width between the spines (Høyberget & Bruton 2008).

Peronopsis scutalis (Hicks, 1872) differs from *Pe. fallax* by having narrower cephalic and pygidial border furrows. The pygidium shows more distinguishing characteristics such as 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 present and the pygidium is spineless.

The figured pygidium (Brøgger 1879, fig. 1a) has a third spine at the pygidial margin, in the middle of the pair of posterolateral spines, and is here excluded from *Pe. fallax*. Linnarsson (1879) figured a cephalon without the characteristic wide border furrow, making an assignment to *Pe. fallax* doubtful. Tullberg (1880) divided *Pe. fallax* in two subspecies: *Agnostus fallax typica* and *Ag. fallax ferox*. The illustrated cephalon for the subspecies *typica* agrees well with *Pe. Fallax*, but the axis of the pygidia is ogival and does not show the characteristic broad form, making their assignment questionable, although an intraspecies variation is possible. Matthew (1886) illustrated *Ag. acadicus*. The cephalon matches that of *Pe. fallax*, but the pygidium in fig. 5b of Matthew (1886) is here assigned to *H. parvifrons*. As discussed above, the illustrated spineless pygidium also has the characteristic lanceolate axis and the distinct forward projection of the posterior border. Matthew (1886) described the new species *Agnostus vir* and the subspecies *Ag. vir concinnus*. Both illustrations show the cephalic and pygidial wide border furrows, and broad pygidial axis with a large axial node and a pair of posterolateral spines. Matthew (1886) distinguished *Ag. vir* from *Pe. fallax* by the form of the anterior glabellar lobe and the trisection segmentation of the posterior thorax segment. *Agnostus vir concinnus* has even more narrow lateral furrows of the glabella. These described characters by Matthew (1886) are here considered to be intraspecies variations of *Pe. fallax*. Because of the above described variability within *Pe. fallax* it is here suggested to avoid the usage of subspecies, as also discussed by Robison (1982).

The pygidium of Matthew (1896) shows a wide border furrow, but the pygidial axis is very broad and too short, thus it is here assigned to *Pe. ferox*. Matthew (1896) illustrated *Ag. fallax concinnus* with the characteristic wide border furrow of the pygidium, but the cephalon has only a narrow border furrow. The cephalon may represent a meraspis stage, making an assignment to *Pe. fallax* questionable.

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

Grabau & Shimer (1910) illustrated a cephalon and pygidium of *Ag. acadicus*. The cephalon is here assigned to *Pe. fallax* because of the typical wide border furrow and the subquadrate, subcircular shape (cf. Robison 1995). Howell (1925) described the new species *Agnostus clarae* given its pygidia with a short axis, and mentioned a connection to *Pe. fallax* and *Pe. ferox*. The illustrated pygidium is subquadrate, and has a wide border furrow, a long axis and a pair of posterolateral spines. Because of the typical characteristics *Ag. clarae* is here assigned to *Pe. fallax*.

In his figure 19, Strand (1929) named the illustrated taxa *Agnostus fallax* and *Agnostus Ag. parvifrons mammillatus*. However, only cephala and pygidia of *H. parvifrons* are illustrated, with an effaced anterior glabellar lobe that is half as long as the cephalon, and non-spinose pygidia that show the distinct forward projection of the posterior border (see the *Hypagnostus parvifrons* section). It is here suggested that Strand (1929) illustrated the wrong species, therefore it is not assigned to *Pe. fallax*.

The illustrated specimens of Hutchinson (1952) and Henningsmoen (1952) are poorly preserved, and no characteristics are visible, therefore any assignment is questionable. Dean (1982) illustrated four cephala and two pygidia of *Pe. fallax minor*, which all have the typical characteristics of *Pe. fallax* such as a wide border furrow, an elongate pygidial axial node and a pair of posterolateral spines. Egorova *et al.* (1982) illustrated several cephala and pygidia of *Pe. fallax*. A cephalon and two pygidia are poorly preserved, so any assignment is here suggested to be questionable (cf. Robison 1995). Samson *et al.* (1990) assigned a cephalon and a pygidium to *Pe. fallax*, but their fig. 5B is here excluded, because of the absence of the pair of pygidial posterolateral spines. Weidner & Nielsen (2009) illustrated a poorly preserved cephalon and pygidium, and their assignment is here considered to be doubtful.

Occurrence. *Peronopsis fallax* is cosmopolitan and has been reported from the middle Cambrian *Ptychagnostus gibbus* Zone to the upper *Ptychagnostus atavus* Zone of Sweden (Westergård 1946; Weidner & Nielsen 2014), North America (Nevada, Utah, North and South Carolina; Robison 1982; Samson *et al.* 1990), Norway (Høyberget & Bruton 2008; Maletz & Steiner 2015) and Denmark (Weidner & Nielsen 2014). *Peronopsis fallax* has also been reported from the upper part of the *Pt. atavus* Zone of New Brunswick and Nova Scotia (Hutchinson 1952), Western Newfoundland (Young & Ludvigsen 1989), Australia (Öpik 1979), England (Rushton 1979), Spain (Gil Cid 1981), Russia (Siberia) (Egorova *et al.* 1982), Eastern Turkey (Dean 1982), Antarctica (Palmer & Gatehouse 1972), Greenland (Robison 1994) and Germany, in erratic boulders (Rudolph 1994). In the present study *Pe. fallax* ranges from the *T. fissus* Zone to the *Pt. atavus* Zone of Eastern Newfoundland.

Peronopsis scutalis (Hicks, 1872)
Figure 6

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* 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* Illing, p. 406, pl. 28, figs 2–5.

1946 *Peronopsis scutalis* (Salter *in* Hicks); Westergård, pp. 41–42 (pars), pl. 4, figs 4–8 (non figs 9–11).

1962 *Peronopsis (Acadagnostus) scutalis* (Salter *in* Hicks); Hutchinson, pp. 72–73, pl. 6, figs 1–5.

1969 *Peronopsis scutalis* (Salter *in* Hicks); Poulsen, pp. 6–7, figs 6A–B.

1979 '*Acadagnostus scutalis*' (Salter); Öpik, pp. 63–64, pl. 2, fig. 5; Text-fig. 17.

? 1979 *Peronopsis scutalis scutalis* (Hicks); Rushton, p. 50, fig. 5C.

1979 *Peronopsis scutalis tenuis* (Illing); Rushton, pp. 50–51, fig. 3G.

non 1982 *Peronopsis scutalis* (Salter *in* Hicks); Egorova *et al.*, p. 67, pl. 58, figs 1–2.

1988 *Peronopsis scutalis* (Hicks) *exarata* (Grönwall); Martin & Dean, pp. 16–17, pl. 4, figs 3, 8.

1994 *Peronopsis scutalis* (Hicks); 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); Rudolph, pp. 154–155, pl. 10, figs 14–15.

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

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

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

2014 *Acadagnostus scutalis* (Hicks) (*s.l.*); Weidner & Nielsen, pp. 62–63, figs 33A–D.

Lectotype. SMA 1050, 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 of the Manuels River Formation (1.96–7.07 m), type locality, Conception Bay South, Newfoundland, Canada. Most specimens were collected from the interval 1.96–3.72 m; in the upper part, specimens of *Pe. scutalis* are rare.

Diagnosis. Cephalon subcircular to subquadrate; glabella approximately two-thirds of cephalon length; long anterior glabellar lobe; small basal lobes; cephalon and pygidium non-spinose; border furrows narrow; pygidium subcircular to semio-vate; 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).

Description. The specimens are mainly well-preserved. The cephala vary in size from 1.3 to 3.4 mm in width and from 1.2 to 3.4 mm in length, and the pygidia vary in size 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 of the collected pygidia show a yellow surface from the pyrite contained in the shale. The cephala and pygidia are characteristically subcircular to subquadrate in shape. Anteriorly the specimens have a broadly rounded anterior glabellar lobe and posteriorly a straight F3 furrow. The pygidial border is narrow in some specimens and wider in others. In some specimens the small, secondary median node is visible, situated at the midpoint of the lanceolate posteroaxis. The pygidial pleural fields are rounded anteriorly and separated by a deep, median, postaxial furrow. The length of the postaxial furrow varies in some specimens.

Remarks. *Peronopsis scutalis* shows morphological variation within populations (Robison 1994; Høyberget & Bruton 2008; Weidner & Nielsen 2014). The cephalon changes less than the pygidia throughout ontogeny and within populations. The cephala have a small axial node on the posterior glabellar lobe. Due to preservation differences, the node is not visible in some specimens. Westergård (1946) described cephala and pygidia from Sweden with a length of 2–3 mm. In 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 matches well with the Swedish specimens described by Westergård (1946).

There is a large variation in length and width in the pygidia (Westergård 1946; Weidner & 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 become deeper throughout ontogeny and in larger specimens (Robison 1994). The pleural fields are separated by a deep, median postaxial furrow. The small secondary median node at the midpoint of the posteroaxis varies from weak to absent, which is probably a matter of preservation (Weidner & Nielsen 2014). *Peronopsis 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 & Bruton 2008).

Hicks (1872) used the name *Pe. scutalis* Salter (1866) in his description, given that Salter (1866) first mentioned the species name in his report. Therefore, especially in older studies, Salter (1866) is listed in several synonymy lists (e.g. in Lake 1906). Salter (1866) mentioned the name *Pe. scutalis* without a description of the species, thus he compiled a *nomen nudum*. According to the ICZN the name and date with the first description of a species are valid, thus Hicks (1872) is listed here. Tullberg (1880) illustrated a pygidium of *Hypagnostus parvifrons*. Typical characteristics of *Pe. scutalis* are a pygidium with a long pygidial axis, tapered posteriorly, and F1 and F2 furrows absent.

Grönwall (1902) described the species *Agnostus exaratus*, figuring a single pygidium with a broad and short pygidial axis, rounded pleural fields and a median postaxial furrow. The broader pygidial axis is here considered an intraspecies variation, and the other characters match those of *Pe. scutalis*. Therefore, the species *Ag. exaratus* is here considered to be a synonym of *Pe. scutalis* (cf.
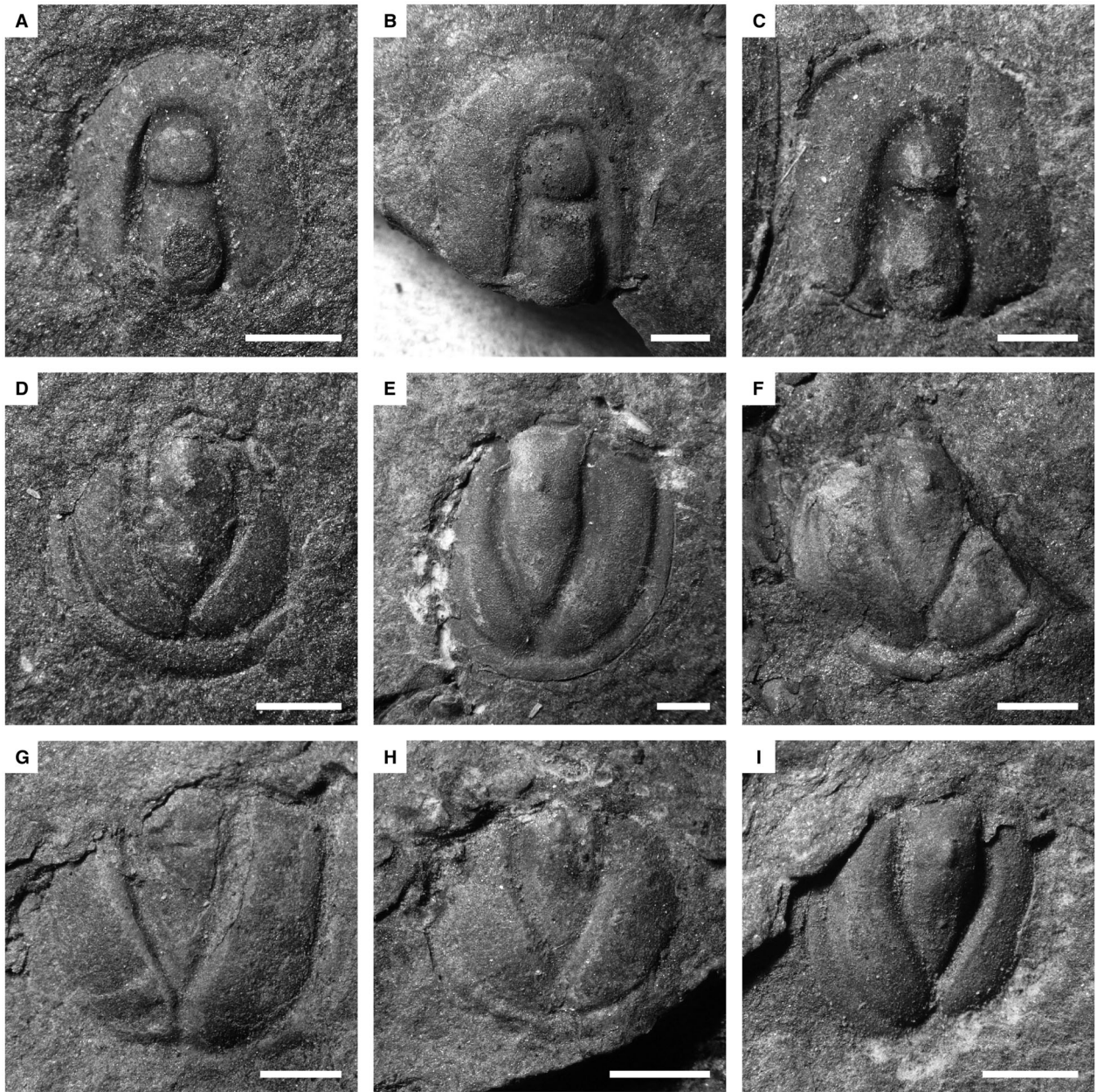
FIG. 6. *Peronopsis scutalis* (Hicks, 1872). A, cephalon (NFM F-1315). B, cephalon (NFM F-1288). C, cephalon (NFM F-1275). D, pygidium (NFM F-1316). E, pygidium (NFM F-1276). F, pygidium (NFM F-1296). G, pygidium (NFM F-1277). H, pygidium (NFM F-1285). I, pygidium (NFM F-1295). Scale bars represent 1 mm.

Høyberget & Bruton 2008). Illing (1915) described the subspecies *Ag. exaratus tenuis*, distinguished from *Pe. scutalis* by its larger size, the subquadrate shape of the anterior glabellar lobe and the narrower and more tapering pygidial axis. The illustrated specimens of *Ag. exaratus tenuis* have a relatively short pygidial axis, which agrees well with *Pe. scutalis*, and hence *Ag. exaratus tenuis* is here suggested to be a synonym of *Pe. scutalis* (cf. Høyberget & Bruton 2008).

The illustrated pygidia of *Peronopsis scutalis* by Westergård (1946, figs 9–11) show a broad axis, posteriorly rounded pleural fields and a forward projection of the broad pygidial border

furrow, and are more typical of *Hypagnostus parvifrons*. Hutchinson (1962) followed the concept of the subgenus *Pe. (Acadagnostus) scutalis*; his illustrated specimens match with *Pe. scutalis* (cf. Høyberget & Bruton 2008). Öpik (1979) and later Rudolph (1994) and Weidner & Nielsen (2014) assigned *scutalis* to the genus *Acadagnostus* Kobayashi, 1939. As discussed under the genus *Peronopsis* (see the *Peronopsis* section) *Pe. scutalis* is non-spinose; thus it is here included into *Peronopsis*.

Rushton (1979) divided *Pe. scutalis* into the subspecies *Pe. scutalis scutalis* and *Pe. scutalis tenuis*. He illustrated a poorly

preserved pygidium of questionable *Pe. scutalis scutalis*, which seems to be compressed at the posterior part. His illustrated complete specimen of *Pe. 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, characteristic of *Pe. scutalis*, and the subspecies of Rushton (1979) is here considered to be a synonym of *Pe. scutalis*.

Egorova *et al.* (1982) illustrated two specimens as *Pe. scutalis* with a semiovate cephalon, an anterior small and subcircular glabellar lobe and a long posterior glabellar lobe. The pygidium shows a long and broad axis. Both illustrated specimens have broad border furrows and axial furrows, uncharacteristic of *Pe. scutalis*. Martin & Dean (1988) described the subspecies *Pe. scutalis exarata* with all specific characters of *Pe. scutalis* and so it is here included into this species (cf. Høyberget & Bruton 2008). Westrop *et al.* (1996) illustrated a cephalon and three poorly preserved pygidia with fragmentary axes. These authors remarked that their few specimens are not sufficient for a confident identification, a view followed here. Høyberget & Bruton (2008) erroneously listed 'Dean 1982' for Martin & Dean (1988) in their synonymy list.

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

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

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; Shergold & Laurie 1997, with modifications).

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

Remarks. The most conspicuous characteristics of *Hypagnostus* are the effacement of the anterior glabellar lobe, the short posterior glabellar lobe and the absence of a median preglabellar furrow (Westergård 1946; Peng & Robison 2000). Intraspecies variations in large populations are specific to the pygidium and include 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 (Peng & Robison 2000). Because of these variable characters, the systematic position and the assignment of synonyms of *Hypagnostus* are still controversial. Shergold *et al.* (1990) and Shergold & Laurie (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 an uncertainty about the monophyly of Spinagnostinae. Both Spinagnostinae and Peronopsidae are primarily determined by the effacement of the anterior glabellar lobe, and this may be a polyphyletically developed characteristic. Westrop *et al.* (1996) considered *Cotalagnostus* to be a synonym of *Hypagnostus*. Peng & Robison (2000) consider *Cotalagnostus* a separate genus, a view followed here. *Cotalagnostus* is distinguished from *Hypagnostus* by an absent glabellar F3 furrow and faint to absent pygidial furrows surrounding the posteroaxis (Shergold & Laurie 1997). *Tomagnostella* was considered a synonym of *Hypagnostus* (e.g. Westergård 1946; Robison 1964). Westrop *et al.* (1996) left both as separate genera on the basis of the pygidial axis character of distinct F1 and F2 furrows, a view followed here.

Hypagnostus parvifrons (Linnarsson, 1869)
Figure 7

1869 *Agnostus parvifrons* Linnarsson, p. 82, pl. 2, figs 56–57.

1880 *Agnostus parvifrons* Linrs.; Tullberg, pp. 34–35 (pars), pl. 2, figs 27–28 (non fig. 26).

1886 *Agnostus acadicus*, Hartt; Matthew, p. 70 (pars), pl. 7, fig. 5b (non fig. 5a).

1886 *Agnostus acadicus*, var. *declivis*, n. var. Matthew, pp. 70–71 (pars), pl. 7, fig. 6b (non fig. 6a).

1886 *Agnostus umbo* Matthew, pp. 71–72, pl. 7, figs 8a–b.

1896 *Agnostus acadicus* Hartt; Matthew, pp. 217–219 (pars), pl. 15, fig. 10b (non fig. 10a).

1896 *Agnostus acadicus* Hartt var. *declivis* Matthew; Matthew, pp. 219–220 (pars), pl. 15, fig. 11b (non fig. 11a, c–d).

1906 *Agnostus parvifrons*, Linnarsson, var. *latelimbatus* Lorenz, p. 84, pl. 4, figs 9a–b; pl. 5, figs 10–11.

1909 *Hypagnostus parvifrons* Linnars. sp.; Jaekel, pp. 398–399, fig. 17.

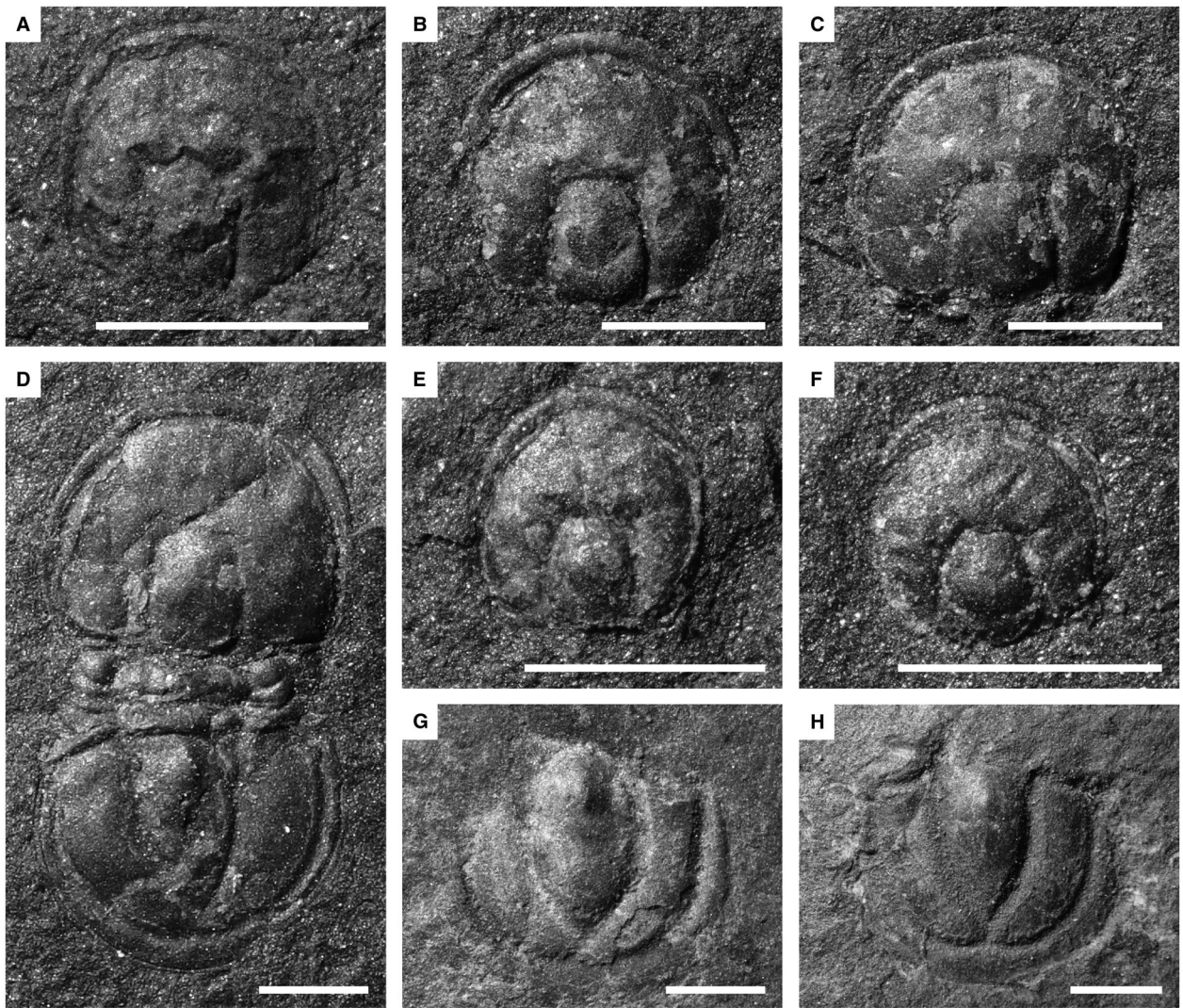1913 *Agnostus parvifrons latelimbatus* Lorenz; Walcott, p. 102, pl. 7, figs 1–1a.

FIG. 7. *Hypagnostus parvifrons* (Linnarsson, 1869). A, cephalon (NFM F-1329). B, cephalon (NFM F-1344). C, cephalon (NFM F-1327). D, complete specimen (NFM F-1326). E, cephalon (NFM F-1330). F, cephalon (NFM F-1347). G, pygidium (NFM F-1357). H, pygidium (NFM F-1328). Scale bars represent 1 mm.

? 1915 *Agnostus parvifrons* Linnarsson; Illing, p. 422, pl. 32, fig. 10.

non 1925 *Agnostus parvifrons punctifer* 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, pp. 346–347, pl. 1, fig. 19.

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

1939 *Hypagnostus (parvifrons)*; Kobayashi, pp. 122–128, fold-out chart in appendix.

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

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

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

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

1962 *Hypagnostus parvifrons* (Linnarsson); Hutchinson, p. 73, pl. 6, figs 6a–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; Öpik, pp. 67–68, pl. 5, figs 1, 7; text-fig. 18.

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

? 1982 *Hypagnostus parvifrons* (Linnarsson); 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 2G–H.

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

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

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

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

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

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

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

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

1997 *H. parvifrons* (Linnarsson); Shergold & Laurie, p. 357, figs 226.5a–b.

2000 *Hypagnostus parvifrons* (Linnarsson); Peng & Robison, pp. 60–63, figs 45.1–11.

2003 *Hypagnostus parvifrons* (Linnarsson); Axheimer & Ahlberg, p. 144, figs 4F–G.

2006 *Hypagnostus parvifrons* (Linnarsson); Fletcher, pp. 66–67, pl. 34, figs 49–50.

2007 *Hypagnosus parvifrons* (Linnarsson); Jago & Cooper, pp. 475–477, figs 2G–H, J–P.

2008 *Hypagnostus parvifrons* (Linnarsson); Høyberget & Bruton, pp. 36–37, pl. 4, figs D–L.

non 2009 *Hypagnostus parvifrons* (Linnarsson); Fatka *et al.*, p. 123, figs 2C–D.

2009 *Hypagnostus parvifrons* (Linnarsson); Weidner & Nielsen, pp. 264–265, figs 14A–B, D–E.

2014 *Hypagnostus parvifrons* (Linnarsson); Weidner & Nielsen, pp. 48–49, figs 21C–D, 22P.

2015 *Hypagnostus parvifrons* Linnarsson; Lin *et al.*, p. 203, pl. 3, fig. 9.

2016 *Hypagnostus* cf. *parvifrons* (Linnarsson); Ahlberg *et al.*, pp. 495–496, fig. 5L.

2016 *H. parvifrons*; Wolvers & Maletz, p. 3, fig. 2.

Lectotype and paralectotype. SGU 4769 as lectotype (cephalon) and SGU 4768 as paralectotype (pygidium), by subsequent designation of Westergård (1946, pl. 4, figs 27–28), refigured by Shergold & Laurie (1997, fig. 226.5a–b). The cephalon and pygidium were illustrated originally by Linnarsson (1869, pl. 2, figs 56–57).

Material. 2 complete specimens, 23 cephala and 11 pygidia (NFM F-1326–F-1361) from the uppermost third of the Manuels River Formation (10.96–15.74 m), type locality, Conception Bay South, Newfoundland, Canada.

Diagnosis. Short oval posterior glabellar lobe not exceeding half the length of the cephalon; cephalon and pygidium non-spinose; 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 & Bruton 2008, with modifications).

Description. The specimens are poorly preserved. Two complete specimens are 4.9 mm and 6.6 mm long, respectively. The cephala vary in size from 1.0 to 5.1 mm in width and from 1.1 to 4.8 mm in length, and the pygidia vary in size 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 m, the specimens 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; when 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.

Remarks. *Hypagnostus parvifrons* shows several variable characters within populations (Westergård 1946; Robison 1964; Westrop *et al.* 1996; Peng & Robison 2000; Høyberget & 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 & Robison 2000; Høyberget & Bruton 2008). The cephalic and pygidial width of the border is another intraspecies variation (Robison 1964; Westrop *et al.* 1996). The pygidial axis is long but variable in length and width (Peng & 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.

Specimens of an ontogenetic series were illustrated by Robison (1964). The morphological changes apart from the increase in size during ontogeny of *H. parvifrons* are moderate. *Hypagnostus parvifrons* is distinguished from closely related species mainly by characteristics of the pygidia. As Weidner & Nielsen (2014) also described, there are no major differences between the cephala of *H. parvifrons* and *H. mammillatus*. *Hypagnostus mammillatus* differs from *H. parvifrons* in having a broad pygidial border, and a raised axis on side view of the pygidium. In contrast, the side view of *H. parvifrons* is slightly convex. Cephala of *H. frontosa* and *H. truncatus* show a longer glabella compared with that of *H. parvifrons*. *Hypagnostus frontosa* differs from *H. parvifrons* in the lack of a forward projection of the pygidial border (Weidner & Nielsen 2014). *Hypagnostus truncatus* differs from *H. parvifrons* in having a wider cephalic border and a longer pygidial axis (Høyberget & Bruton 2008). As also discussed

under *Pe. fallax* (see above), Hartt (*in* Dawson 1868) described the species *Agnostus acadicus*. The sampled cephalon and pygidium of Dawson (1868) were later revised by Öpik (1979) and Robison (1995), who proposed that the questionable type pygidium of Hartt be assigned to *Hypagnostus parvifrons* (Linnarsson, 1869). In the present study the suggestion of Høyberget & Bruton (2008) is followed, as shown under *Pe. fallax*.

Tullberg (1880) figured two complete specimens and a single pygidium with a long, posteriorly tapered pygidial axis, in which 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 *Pe. scutalis*. Matthew (1886) illustrated a cephalon and pygidium of *Ag. acadicus* with the specific characters of *H. parvifrons*. However, the figured cephalon is here excluded from *H. parvifrons* because of its subquadrate shape, wider border furrow and the presence of an anterior glabellar lobe. The specimen in figure 5a of Matthew (1886) is here assigned to *Peronopsis fallax* (see the *Pe. fallax* section). Matthew (1886) also described the new subspecies *Ag. acadicus declivis*. The pygidium figured by Matthew (1886) shows the characters of *H. parvifrons* (cf. Peng & Robison 2000). The figured cephalon in Tullberg (1880) shows a shorter glabella than in Matthew (1886), but an anterior glabellar lobe is also visible. Therefore, it is here not assigned to *H. parvifrons*. Furthermore, Matthew (1886) described the new species *Agnostus umbo*. Its cephalon shows an oval posterior glabellar lobe, an effaced anterior glabellar lobe and a narrow border furrow. The figured pygidium (Tullberg 1880) shows the same character as Matthew's (1886) figures 5b and 6b; *Ag. umbo* is here considered to be a synonym of *H. parvifrons*. Matthew (1896) also illustrated the species *Ag. acadicus* and the subspecies *Ag. acadicus declivis*. The figured pygidia of *Ag. Acadicus* (Matthew 1896, fig. 10b) and the subspecies (fig. 11b) are here included in *H. parvifrons*, because they show the typical characters as described above. The figured cephalon in Matthew (1896) matches well with the figured cephalon in Matthew (1886) and is therefore referred to *Pe. fallax*. The cephalon in Matthew (1896) shows an anterior glabellar lobe and is therefore not considered to be *H. parvifrons*. One of the pygidia of *Ag. acadicus declivis* figured by Matthew (1896) shows faint horizontal furrows across the pygidial pleural fields and the anteroaxis, and another pygidium has five pits on the axis near the axial node. Because of these characters, the specimens shown in figs 11c–d of Matthew (1896) are excluded from *H. parvifrons*. Lorenz (1906) described the new subspecies *Agnostus parvifrons latelimbatus*, which he distinguished from *H. parvifrons* by a broader pygidial posterior border, although not as broad as in *H. mammillatus*. Its cephalon agrees closely with that of *H. parvifrons*. The pygidia figured by Lorenz (1906) have a relatively broad border, typical of *H. parvifrons*, although Lorenz (1906, fig. 9b) shows only a side view of a flat specimen, as shown by Høyberget & Bruton (2008, pl. 4, fig. L). In contrast, on side view of *H. mammillatus* the pygidium is raised. The characters described by Lorenz (1906) are here interpreted as intraspecies variations and therefore the separations into subspecies are unjustified.

Walcott (1913) figured a cephalon and a pygidium of the subspecies *Ag. parvifrons latelimbatus* with the characteristics of *H. parvifrons*. The specimens figured by Illing (1915) are poorly preserved, and a species assignment is here considered doubtful. The subspecies *Ag. 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, and a side view of the pygidium with typical features of *H. mammillatus*. Strand (1929) described *Pe. fallax*, but figured several species of *H. parvifrons*. Therefore, the figured specimens of *Pe. fallax* are here assigned to this species. Cobbold & Pocock (1934) figured pygidia with a broad border and a prominent axial node, 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. The figured specimens fall within the morphology of *H. parvifrons*, and therefore *H. clipeus* is considered a synonym.

Rasetti (1948) described the new species *H. métisensis* to be very close to *H. parvifrons*, from which it differs only by a narrower cephalic border. However, the figured specimens have all of the characters of *H. parvifrons*. In addition, it is here suggested that Rasetti's (1948) described variation of the cephalic border, is an intraspecies variation and therefore *H. métisensis* is here assigned as 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 assignment to *H. parvifrons* is questionable (cf. Peng & Robison 2000). Öpik (1979) figured one complete specimen and a pygidium of *H. clipeus* Whitehouse, 1939. The cephalon has the same characters as *H. parvifrons* 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, both here suggested to be intraspecies variations of *H. parvifrons* (cf. Peng & Robison 2000). All illustrated specimens of Egorova *et al.* (1982) and Samson *et al.* (1990) are poorly preserved and their assignment to *H. parvifrons* is here considered doubtful (cf. Peng & Robison 2000). Fatka & Kordule (1992) figured a complete specimen of *H.* cf. *parvifrons*, which is here included into *H. mammillatus*, with its broader pygidial border. For the same reason, Rudolph's (1994) figured specimens of *H. parvifrons parvifrons* are here included into *H. mammillatus*. As discussed above, Fatka *et al.* (2009) figured specimens that agree with those of Fatka & Kordule (1992) and are here included into *H. mammillatus*. *Hypagnostus 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 *Pt. atavus* Zone to the *Pt. punctuosus* Zone) (Høyberget & Bruton 2008).

Occurrence. *Hypagnostus parvifrons* is a widespread species and has been reported from the middle Cambrian lower *Pt. atavus* Zone of Sweden (Öland; Weidner & Nielsen 2009), the *Pt. atavus* Zone of Sweden, North and South Carolina, USA, and Antarctica (Westergård 1946; Samson *et al.* 1990; Jago & Cooper 2007; Ahlberg *et al.* 2016), the upper part of the

Pt. atavus Zone of New Brunswick, Québec, Utah, Texas and New York, USA, Australia, Greenland, England and Denmark (Rasetti 1948; Robison 1964, 1994; Öpik 1979; Palmer *et al.* 1984; Weidner & Nielsen 2014), the *Pt. atavus* Zone to the *Pt. punctuosus* Zone of Russia (Siberia) and Norway (Egorova *et al.* 1982; Høyberget & Bruton 2008; Wolvers & Maletz 2016) and the *Pt. atavus* Zone to the *Lejopyge laevigata* Zone of Japan, Argentina and China (Kobayashi 1939; Tortello & Bordonaro 1997; Peng & Robison 2000). The species was also reported from East Asia (Lorenz 1906). In the present study *H. parvifrons* ranges from the *H. parvifrons* Zone to the *Pt. atavus* Zone of Eastern Newfoundland.

Family PTYCHAGNOSTIDA Kobayashi, 1939

Genus PTYCHAGNOSTUS Jaekel, 1909

Type species. *Agnostus punctuosus* Angelin, 1851, by original designation.

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 Shergold & Laurie 1997; Peng & 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*, the type species of *Ptychagnostus* (Jaekel, 1909), was originally described from an anthraconite boulder from Andrarum, Scania, Sweden. The genus characteristics of *Ptychagnostus,* such as spines, genal scrobiculation and surface granulation, are highly variable within populations (Robison 1984; Peng & 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 fulfils the requirements for good index fossils in the Cambrian as discussed by Peng & Robison (2000), such as short stratigraphic ranges, wide palaeogeographic distribution in open-marine facies and abundant occurrence.

Ptychagnostus punctuosus (Angelin, 1851)
Figure 8

1851 *Agnostus punctuosus* Angelin, p. 8, pl. 6, fig. 11.
1872 *Agnostus scutalis*, Salter; Hicks, p. 175 (pars), pl. 5, figs 9–10 (non figs 11–14).
1875 *Agnostus punctuosus* Angelin; Brøgger, p. 576, pl. 25, fig. 2.
1879 *Agnostus punctuosus* Angelin; Brøgger, p. 67, pl. 6, figs 12a–b.
1880 *Agnostus punctuosus* Ang.; Tullberg, pp. 17–18, pl. 1, figs 5a–d.
1896 *Agnostus punctuosus* Angelin; Matthew, p. 232, pl. 16, figs 11a–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)*; Kobayashi, pp. 152–153, fold-out chart in appendix.
1944 *Ptychagnostus punctuosus* (Angelin); Shimer & Shrock, p. 600, pl. 251, fig. 20.
1946 *Ptychagnostus (Ptychagnostus) punctuosus* (Angelin); 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); Poulsen, pp. 4–5, figs 4A–B.
1972 *Ptychagnostus (Ptychagnostus) punctuosus* (Angelin); Fletcher, pl. 5, figs 1–2.
1979 *Ptychagnostus punctuosus fermexilis* Öpik, p. 92, pl. 41, figs 1–5.
1979 *Ptychagnostus punctuosus punctuosus* (Angelin); 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); Ergaliev, pp. 70–71, pl. 1, fig. 25.
1981 *Ptychagnostus punctuosus* (Angelin); Allen *et al.*, pl. 16, fig. 1.
1982 *Ptychagnostus punctuosus* (Angelin); 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, fig. 4D–G.
1984 *Ptychagnostus punctuosus* (Angelin); Robison, pp. 33–35, figs 20.1–6b.
1985 *Ptychagnostus punctuosus fermexilis* Öpik; Xiang & Zhang, p. 73, pl. 21, figs 9, 12.
1985 *Ptychagnostus punctuosus punctuosus* (Angelin); Xiang & Zhang, pp. 73–74, pl. 20, figs 4–5, 11, 15.
1988 *Ptychagnostus punctuosus* (Angelin); Laurie, p. 172, fig. 1A–F.
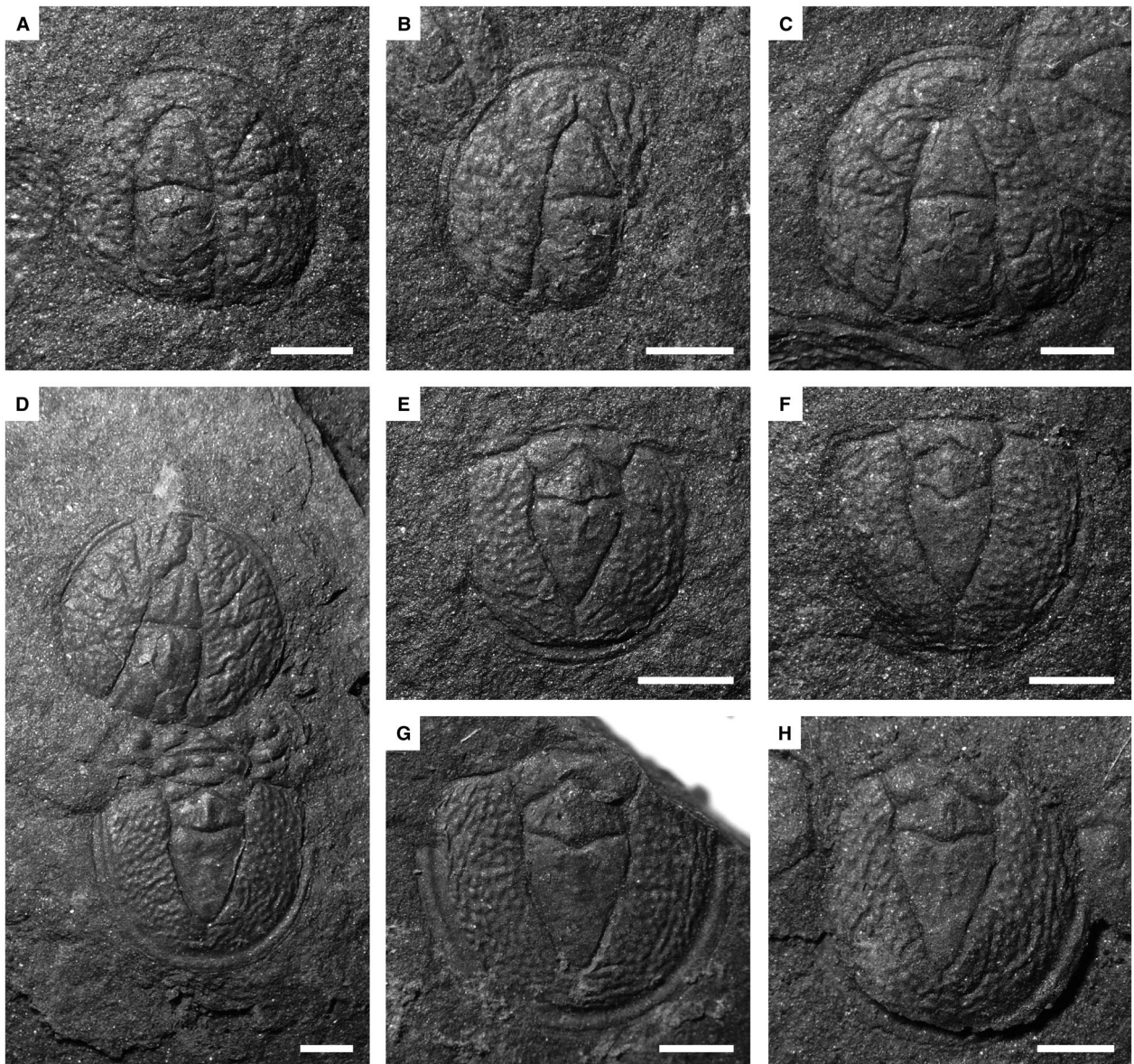v 1988 *Ptychagnostus punctuosus* (Angelin); Martin & Dean, p. 17, pl. 4, figs 5–6, 10.

FIG. 8. *Ptychagnostus punctuosus* (Angelin, 1851). A, cephalon (NFM F-1425). B, cephalon (NFM F-1423). C, cephalon (NFM F-1363). D, complete specimen (NFM F-1362). E, pygidium (NFM F-1421). F, pygidium (NFM F-1422). G, pygidium (NFM F-1364). H, pygidium (NFM F-1424). Scale bars represent 1 mm.

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

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

1997 *Ptychagnostus punctuosus* (Angelin); Shergold & Laurie, p. 351, fig. 223.1a–b.

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

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

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

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

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

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

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

2008 *Ptychagnostus punctuosus* (Angelin); Høyberget & 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, fig. 3E–F.
2014 *Ptychagnostus punctuosus punctuosus* (Angelin); Rees et al., p. 19, fig. 1.12d–e, g.
2016 *P. punctuosus*; Wolvers & Maletz, p. 3, fig. 2.

Lectotype. AR 9539, by subsequent designation of Westergård (1946, p. 78, pl. 12, figs 3a–b).

Material. 2 complete specimens, 40 cephala and 41 pygidia (NFM F-1362–F-1444) from the upper part (16.76–18.06 m) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

Diagnosis. Cephalon subcircular to slightly subelliptical with narrow borders; genae strongly scrobiculate and granulose; posterior glabellar lobe trapezoid; cephalon and pygidium non-spinose; 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 moderately developed (based on Öpik 1979; Robison 1984; Laurie 1988, with modifications).

Description. The specimens are well-preserved. Complete specimens are 9.0 mm and 11.1 mm long, respectively. The cephala vary in size from 3.5 to 4.3 mm in width and from 3.6 to 4.4 mm in length, and the pygidia vary in size from 3.7 to 4.2 mm in width and from 3.5 to 4.3 in length. All cephala and pygidia show a characteristic granulation with visible median preglabellar furrow and scrobiculate genae. The anterior glabellar lobe is semiovate to triangular. Some specimens show a sulcus, which extends to the median preglabellar furrow. This sulcus is either a matter of preservation or an intraspecies morphological variation.

Remarks. *Ptychagnostus punctuosus* 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 coarse genal surface granulation, prominent genal scrobicules and a longer and more defined pygidial axis. The median postaxial furrow is clearly developed in the meraspis stage and becomes fainter throughout ontogeny, as observed by Lake (1906) and Illing (1915). Axheimer & Ahlberg (2003) proposed five different ontogenetic stages for the pygidia of *Pt. punctuosus* based on data from nine pygidia and four cephala. In this model they defined the change in the stages from meraspis to holaspis based on the previously mentioned characteristics. Although the definition is detailed, the low number of observed specimens is problematical for statistical analysis. In addition, variation of the diagnostic characters depends 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 accentuated 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 noted by Westergård (1946).

Subgenera of *Ptychagnostus* and subspecies of *Pt. punctuosus* were commonly distinguished in the past (e.g. Westergård 1946; Öpik 1979; Berg-Madsen 1984). The most frequently described subspecies are *Pt. punctuosus punctuosus* and *Pt. punctuosus affinis*. Öpik (1979) introduced the subspecies *Pt. 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 *Pt. punctuosus*. Also the illustrations of the species match with *Pt. punctuosus*, therefore *Pt. punctuosus fermexilis* is here assigned as a synonym of *Pt. punctuosus* (cf. Peng & Robison 2000).

The wide morphological variability between ontogenetic stages and within populations challenges the subdivision into subspecies, and it is here suggested to avoid the usage of subspecies, as also suggested by Robison (1984). The closely related species *Pt. affinis* differs from *Pt. punctuosus* by the absence of genal granules and by the weakly developed pygidial granules on the pleural fields. *Ptychagnostus atavus* differs in its absence of granules on the genae and on the pygidial pleural fields.

The description of the species *Agnostus scutalis* and the two pygidia of Salter (*in* Hicks 1872, pl. 5, figs 9–10) match with *Pt. punctuosus*. The other figures of Salter (*in* Hicks 1872, 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 the Manuels River Formation (beds 95–120) and agreed with Howell's record, but without proper description or illustrations. The species was also mentioned by Jaekel (1909), also without descriptions or figures.

Specimens of Hutchinson (1962), GSC 13048, and Martin & Dean (1988), GSC 83300–83302, originating from Manuels River were examined. Their host lithology differs significantly from that of the specimens collected for the present study. Hutchinson's (1962) material appears to originate from loose samples from the east bank of the Manuels River, as stated in his fieldbook, instead of the west bank, as for ours. The material of Martin & Dean (1988) appears to have a similar lithology to that of Hutchinson, and its origin is therefore also uncertain. Both studies (Hutchinson 1962; Martin & Dean 1988) lack litchologs or maps, they only postulate that their specimens are from the west bank of the river. Compared with the material studied here, and going by the notes in the fieldbook from Hutchinson (1962), the stated origin is doubtful. The precise level of origin of these specimens remains uncertain, as already mentioned by Austermann (2016).

Occurrence. *Ptychagnostus punctuosus* has been reported globally from the middle Cambrian *Pt. punctuosus* Zone of Nevada, Utah and New York, USA; Wales, England, Greenland, Norway, Sweden, Denmark, Germany (in erratic boulders), Kazakhstan, Russia (Siberia), China, Japan and Australia (Illing 1915; Kobayashi 1939; Westergård 1946; Poulsen 1969; Öpik 1979; Ergaliev 1980; Allen et al. 1981; Egorova et al. 1982; Berg-Madsen 1984; Robison 1984; Rudolph 1994; Peng & Robison 2000; Weidner et al.

2004; Høyberget & Bruton 2008; Rees *et al.* 2014; Wolvers & Maletz 2016). In the present study *Pt. punctuosus* occurs in the *Pt. punctuosus* Zone of Eastern Newfoundland.

Ptychagnostus affinis (Brøgger, 1879)
Figure 9

1879   *Agnostus punctuosus*, Ang. var. *affinis* Brøgger, p. 68, pl. 5, fig. 2a–b.
1946   *Ptychagnostus (Ptychagnostus) punctuosus affinis* (Brögger); 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); Öpik, pp. 91–92, pl. 39, fig. 8; pl. 40, figs 2–7.
1979   *Ptychagnostus mesostatus* Öpik, pp. 97–98, pl. 40, fig. 8; pl. 41, figs 6–7.
1984   *Ptychagnostus affinis* (Brøgger); Robison, pp. 16–17, fig. 9.1–8.
1988   *Ptychagnostus affinis* (Brøgger); Laurie, pp. 172–173, fig. 2A–E.
1994   *Ptychagnostus affinis* (Brøgger); Robison, p. 55, figs 10.5, 27.1–2.
? 1994   *Ptychagnostus affinis* (Brøgger); Rudolph, pp. 110–111, pl. 4, figs 15–16.
2000   *Ptychagnostus affinis* (Brøgger); Peng & Robison, pp. 68–69, fig. 51.
2003   *Ptychagnostus affinis* (Brögger); Axheimer & Ahlberg, p. 147, figs 4O–P, 5A.
2007   *Ptychagnostus affinis*; Ahlberg *et al.*, p. 10, fig. 3H–J.
2008   *Ptychagnostus affinis* (Brøgger); Høyberget & 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); Weidner & Nielsen, figs 9A–C, 10C.
2010   *Ptychagnostus affinis* (Brøgger); Jago & Bentley, p. 476, fig. 6e–h.
2014   *Ptychagnostus affinis* (Brøgger); Weidner & Nielsen, pp. 36–37, fig. 13A–D.
? 2017   *Ptychagnostus* cf. *affinis*; Hammer & Svensen, p. 222, fig. 6B, F.

Lectotype. PMO 28148, originally figured by Brøgger (1879, pl. 5, fig. 2a), refigured and designated as lectotype by Høyberget & Bruton (2008, pl. 7, fig. O).

Material. 1 complete specimen, 48 cephala and 50 pygidia (NFM F-1445–F-1543) from the interval 14.92–15.32 m of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

Diagnosis. Cephalic genae smooth to moderately scrobiculate; posterior glabellar lobe trapezoid; cephalon and pygidium non-spinose; 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 & Bruton 2008, with modifications).

Description. The specimens are mainly well-preserved. The complete specimen is 11.4 mm long. The cephala vary in size from 2.7 to 5.2 mm in width and from 2.6 to 5.4 mm in length. The pygidia vary in size from 3.1 to 4.7 mm in width and from 3.3 to 4.8 mm in length. All cephala are scrobiculate with a median preglabellar furrow. Some specimens show a cephalic axial node situated at the midpoint of the posterior glabellar lobe, on other specimens the node is missing, which possibly 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 the midpoint of the posteroaxis. The median postaxial furrow becomes fainter in larger specimens and the pygidial pleural fields are weakly granulated.

Remarks. This species is closely related to *Ptychagnostus atavus*, *Pt. punctuosus* and *Pt. intermedius* (Tullberg, 1880). *Ptychagnostus affinis* differs from *Pt. atavus* by its weakly developed pygidial granules on the pleural fields compared with the smooth pygidia of *Pt. atavus* (Westergård 1946; Robison 1984; Peng & Robison 2000). The posteroaxis of *Pt. atavus* is more convex. *Ptychagnostus affinis* shows a lanceolate posteroaxis with 2–5 pairs of lateral impressions, in some Swedish specimens (Weidner & Nielsen 2009). Some specimens of *Pt. atavus* have a crescentic pair of furrows, located opposite the anterior glabellar lobe, which is an intraspecies variation. These furrows have not been described or figured for *Pt. affinis*. *Ptychagnostus punctuosus* is distinguished from *Pt. affinis* by strong granulation on cephala and pygidia (Westergård 1946; Robison 1984; Høyberget & Bruton 2008). The axial node on the cephalon is more prominent and the pygidial posteroaxis is more rounded than in *Pt. affinis* (Høyberget & Bruton 2008). This indicates that *Pt. affinis* is an intermediate form between *Pt. atavus* and *Pt. punctuosus*, as discussed by several authors (Westergård 1946; Robison 1984; Peng & Robison 2000; Axheimer & Ahlberg 2003; Høyberget & Bruton 2008). *Ptychagnostus intermedius* differs from *Pt. 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 produce the typical pentagonal M2 in outline (Robison 1984).

Brøgger (1879) described the subspecies *Agnostus punctuosus affinis* on the basis of a few cephala. He postulated that these cephala have the same characters as in *Pt. punctuosus*, but the pygidia in *Pt. punctuosus* have a stronger granulation compared with *Ag. punctuosus affinis*, together with a fainter granulation on the pygidial pleural fields. The drawings of the subspecies agree closely with *Pt. affinis*. Between the description of *Pt. affinis* by Brøgger (1879) and that by Westergård (1946) is a gap of 67 years, with no other known studies of *Pt. affinis*. Subgenera of *Ptychagnostus* and subspecies of *Pt. punctuosus* were commonly used in the past (e.g. Westergård 1946; Palmer 1968; Öpik 1979).
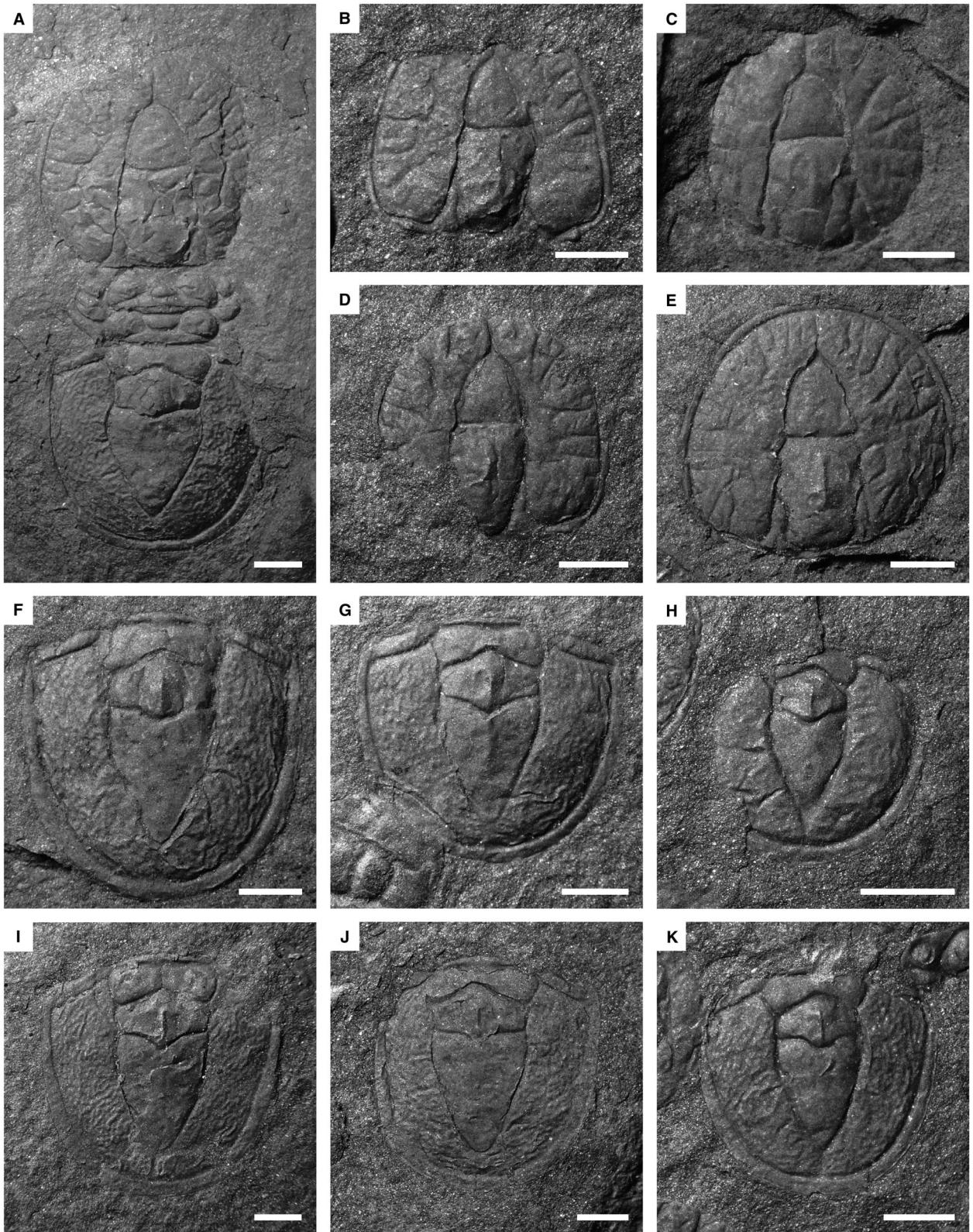
FIG. 9. *Ptychagnostus affinis* (Brøgger, 1879). A, complete specimen (NFM F-1472). B, cephalon (NFM F-1507). C, cephalon (NFM F-1450). D, cephalon (NFM F-1508). E, cephalon (NFM F-1445). F, pygidium (NFM F-1446). G, pygidium (NFM F-1463). H, pygidium (NFM F-1509). I, pygidium (NFM F-1447). J, pygidium (NFM F-1485). K, pygidium (NFM F-1510). Scale bars represent 1 mm.

Palmer's (1968, figs 26–27) specimens are here excluded from *Pt. affinis* because the pygidial posteroaxis has an ogival form and there are no faint granules, uncharacteristic of *Pt. affinis*. The cephalon of Palmer (1968) has a crescentic pair of furrows on the opposite side of the anterior glabellar lobe and a pair of pygidial posterolateral spines as in *Pt. affinis*. Öpik (1979) erected the species *Ptychagnostus mesostatus* on the basis of one complete exoskeleton and one pygidium. The species was defined by a posterior glabellar lobe with parallel flanks, characters that are not visible in the illustrations, making the species questionable (cf. Peng & Robison 2000). Robison (1984) elevated *Pt. punctuosus affinis* to species rank. Rudolph (1994) figured two cephala, here considered questionable, because characteristics are not visible (cf. Peng & Robison 2000). Hammer & Svensen (2017) figured a cephalon with characteristic trapezoid shape of the posterior glabellar lobe and smooth scrobiculate cephalic genae, and a poorly preserved pygidium without weak granulation of the pleural fields and without hexagonal M2. Although the cephalon is convincing, the assignment of the pygidium is here considered doubtful.

Occurrence. *Ptychagnostus affinis* is widespread and was reported from the middle Cambrian *Pt. atavus* Zone of China (Peng & Robison 2000), the upper part of the *Pt. atavus* Zone of Greenland and Denmark (Robison 1994; Weidner & Nielsen 2014) and the upper part of the *Pt. atavus* Zone to the *Pt. punctuosus* Zone of Nevada and Utah, USA; Sweden, Norway and Australia (Westergård 1946; Öpik 1979; Robison 1984; Høyberget & Bruton 2008; Weidner & Nielsen 2009). The species is also reported from Germany, in erratic boulders (Rudolph 1994). In the present study *Pt. affinis* occurs in the upper part of the *Pt. atavus* Zone of Eastern Newfoundland.

Ptychagnostus atavus (Tullberg, 1880)
Figure 10

1880 *Agnostus atavus* Tullberg, pp. 14–15, pl. 1, figs 1a–d.
non 1929 *Agnostus atavus* Tbg.; Strand, p. 344, pl. 1, fig. 20.
1946 *Ptychagnostus (Ptychagnostus) atavus* (Tullberg); Westergård, pp. 76–77 (pars), pl. 11, figs 8–18, 22–25 (non figs 19–21).
1962 *Ptychagnostus atavus* (Tullberg); Hutchinson, pp. 83–84, pl. 8, figs 16–22; pl. 9, figs 1–8.
1979 *Ptychagnostus atavus* (Tullberg); 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* Öpik, pp. 94–95, pl. 42, figs 5–6.
1979 *Ptychagnostus intermedius* (Tullberg); Öpik, p. 95, pl. 41, fig. 8.
1979 *Ptychagnostus (Acidusus) navus* Öpik, pp. 101–102, pl. 46, fig. 1.
1980 *Ptychagnostus atavus* (Tullberg); Ergaliev, pp. 67–69, pl. 1, figs 13–17.
1982 *Ptychagnostus atavus* (Tullberg); Egorova et al., pp. 63–64 (pars), pl. 6, fig. 7; pl. 7, fig. 6.; pl. 11, figs 1–3; pl. 13, fig. 13; (non pl. 51, fig. 11); pl. 55, figs 16, 18, 20–21.
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); Laurie, p. 180, fig. 5A–F.
1994 *Ptychagnostus atavus* (Tullberg); Robison, pp. 55–56, fig. 27.5–6.
? 1994 *Acidusus atavus* (Tullberg); Rudolph, pp. 113–114, pl. 3, fig. 3.
1994 *Acidusus sterleyi* Rudolph, pp. 116–117, pl. 3, figs 6–10.
1996 *Ptychagnostus (s.l.) atavus* (Tullberg); Westrop et al., pp. 816–817, fig. 15.1–4.
2000 *Ptychagnostus atavus* (Tullberg); Pegel, p. 1013, fig. 11.13.
2000 *Ptychagnostus atavus* (Tullberg); Peng & Robison, pp. 69–70, fig. 52.1–8.
2003 *Ptychagnostus atavus* (Tullberg); Axheimer & Ahlberg, p. 147, fig. 5B–C.
2006 *Ptychagnostus atavus*; Axheimer, fig. 6G–H.
2006 *Acidusus atavus* (Tullberg); Fletcher, pp. 66–67, pl. 34, figs 43–44.
2007 *Ptychagnostus atavus* (Tullberg); Ahlberg et al., pp. 710–713, figs 2.1–12.
2007 *Ptychagnostus atavus* (Tullberg); Babcock et al., pp. 88–89, figs 6B–D, 7B.
2008 *Ptychagnostus atavus* (Tullberg); Høyberget & Bruton, pp. 49–50, pl. 7, figs G–M.
2009 *Acidusus atavus* (Tullberg); Weidner & Nielsen, pp. 259–260, figs 8A–D, 10A–B.
2014 *Acidusus atavus* (Tullberg); Weidner & Nielsen, pp. 32–35, figs 9, 10A–D, 11A–H, 12F–H.
2015 *Ptychagnostus atavus* (Tullberg); Hong & Choi, pp. 378–388, figs 2.1–8.
2016 *P. atavus* (Tullberg); Ahlberg et al., pp. 495–496, figs 5G–J, O.
2016 *P. atavus*; Wolvers & Maletz, p. 3, fig. 2.
2017 *Ptychagnostus atavus* (Tullberg); Babcock et al., p. 383, fig. 1.2.
2017 *Ptychagnostus atavus* (Tullberg); Beresi et al., p. 700, fig. 6K.
2018 *Ptychagnostus atavus* (Tullberg); Choi, p. 6, fig. 5a–b.
2019 *Ptychagnostus atavus* (Tullberg); Cuen-Romero et al., pp. 100–103, figs 8A–D.
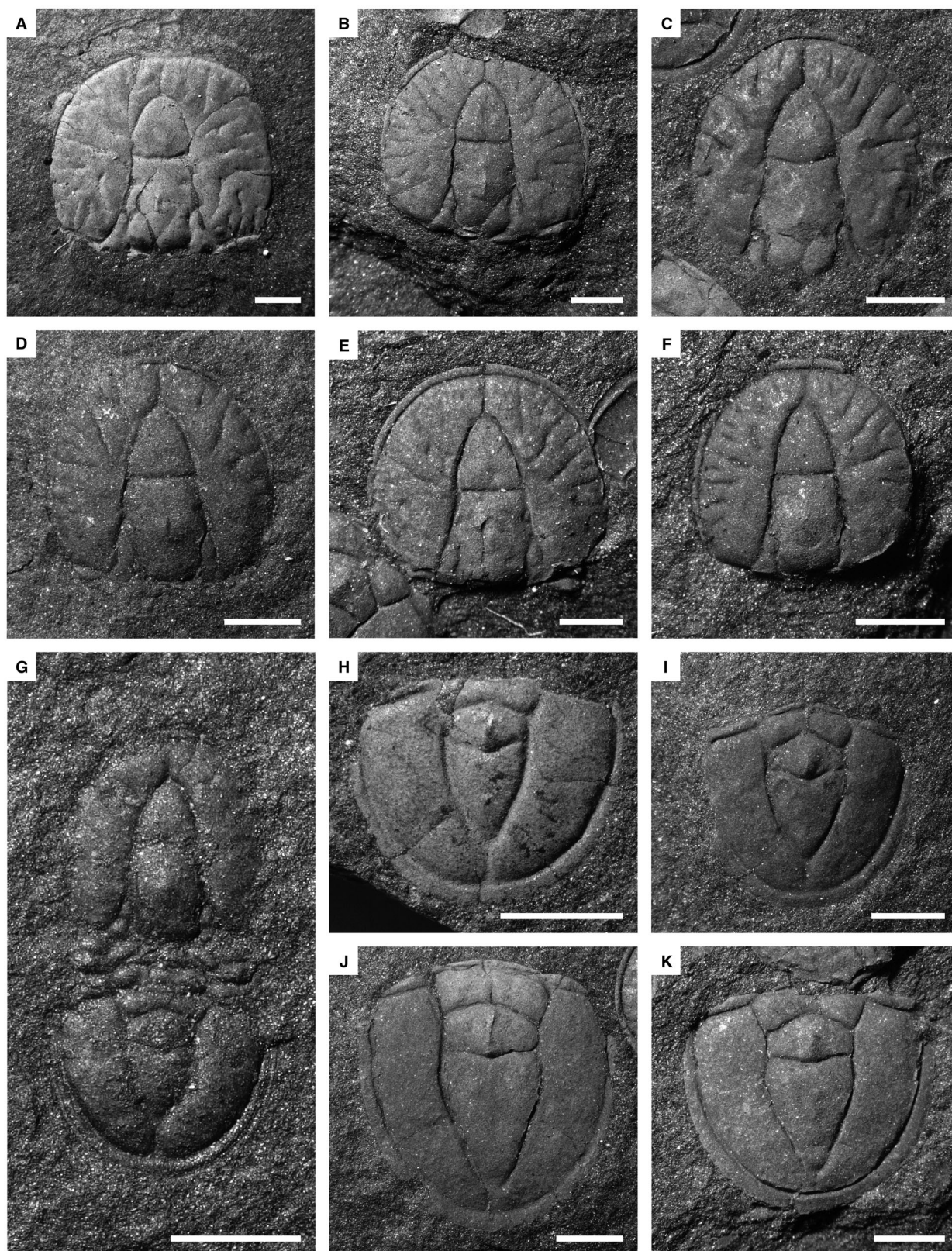
FIG. 10. *Ptychagnostus atavus* (Tullberg, 1880). A, cephalon (NFM F-1545). B, cephalon (NFM F-1590). C, cephalon (NFM F-1600). D, cephalon (NFM F-1547). E, cephalon (NFM F-1544). F, cephalon (NFM F-1584). G, complete specimen (NFM F-1548). H, pygidium (NFM F-1585). I, pygidium (NFM F-1601). J, pygidium (NFM F-1602). K, pygidium (NFM F-1546). Scale bars represent 1 mm.

Lectotype. LO 354T, by subsequent designation of Westergård (1946, p. 130, pl. 11, fig. 8), originally figured and designated as syntype by Tullberg (1880).

Material. 3 complete specimens, 49 cephala and 55 pygidia (NFM F-1544–F-1650) from the interval 11.90–12.08 m of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

Diagnosis. Cephalon convex; genae smooth to moderately scrobiculate; posterior glabellar lobe trapezoid; cephalon and pygidium non-spinose; 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 1984; Peng & Robison 2000, with modifications).

Description. The specimens are mainly well-preserved, with all complete specimens preserved as moulds. The complete specimens are 3.7, 5.8 and 8.5 mm long, respectively. The cephala vary in size from 3.4 to 5.0 mm in width and from 3.1 to 4.7 mm in length, and the pygidia vary in size 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 typical characters such as scrobiculate genae, more prominent in larger specimens, 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 the 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 differences in the position of the glabellar node and the occurrence of the F2 furrow are probably intraspecies variations. The basal lobes are mostly elongate and entire. Most of the pygidia have 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 posteroaxis.

Remarks. Ptychagnostus atavus is a common ptychagnostid species. It shows wide variations in morphology during different ontogenetic stages and within populations (e.g. Westergård 1946; Hutchinson 1962; Robison 1982; Peng & Robison 2000; Ahlberg *et al.* 2007; Weidner & Nielsen 2014). The cephala vary less than the pygidia throughout ontogeny. The meraspis stage is characterized by smooth to weak scrobiculate genae, stronger in the holaspis stage. Also, the median preglabellar furrow (as is the median postaxial furrow) is clearly developed in the meraspis stage and becomes increasingly fainter throughout ontogeny (Westergård 1946; Robison 1982). The pygidial axis grows from a short and lanceolate to a longer and more ogival shape (Fig. 10G–K). The F2 furrow is not yet developed in the meraspis stage and the axial node is often fainter than in the holaspis stage. Some cephala have a crescentic pair of furrows, which may vary in size and shape. These furrows are located opposite the anterior glabellar lobe (Robison 1982), for example, from Sweden (Westergård 1946), western North America (Robison 1982), western Newfoundland (Westrop *et al.* 1996), Hunan in China (Peng & Robison 2000) and Bornholm, Denmark (Weidner & Nielsen 2014). There is also considerable variation in the position of the axial node on the cephala: it can be found on the middle of the posterior glabellar lobe, and the vertical level on M2 varies from the F1 to the F2 furrows (e.g. Westrop *et al.* 1996; Ahlberg *et al.* 2007; Weidner & Nielsen 2009).

Other intraspecies variations involve 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. When the node is situated in the middle of M2, the F2 furrow is less rounded than when 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 as to whether 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 *Pt. atavus* is controversial, as discussed by many authors (Westergård 1946; Öpik 1979; Robison 1982, 1984; Laurie 1988; Ahlberg *et al.* 2007; Weidner & Nielsen 2014). Jaekel (1909) erected *Ptychagnostus* and assigned *Pt. atavus* to this genus. Later, Westergård (1946) erected the subgenus *Ptychagnostus* (*Ptychagnostus*) and Öpik (1979) the subgenus *Ptychagnostus* (*Acidusus*), with the main distinguishing character being 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, which, in contrast, had been noted by Öpik (1979). Laurie (1988) assigned the species *atavus* to *Acidusus*, but mentioned that *atavus* is not a typical representative of *Acidusus* because some specimens have a crescentic pair of furrows on the cephalic genae. Rudolph (1994), Fletcher (2006) and Weidner & Nielsen (2009, 2014) also assigned *atavus* to *Acidusus*. In contrast, it is here suggested that *atavus* be assigned to *Ptychagnostus*. *Acidusus* is here considered to be a synonym of *Ptychagnostus* (cf. Peng & Robison 2000) because of the variable morphological characters described above. Westergård (1946) and Robison (1994) postulate that the species *Pt. atavus*, *Pt. affinis* and *Pt. punctuosus* form a continuous evolutionary series.

The closely related species *Pt. affinis* differs from *Pt. atavus* by its weakly developed pygidial granules on the pleural fields. Isolated cephala of these species, therefore, may be difficult to distinguish. *Ptychagnostus punctuosus* differs by the strong granulation on the cephalic genae and the pygidial pleural fields. *Ptychagnostus 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 excluded from *Pt. atavus* because the posterior glabellar lobe is atypically rounded. Westergård's (1946, pl. 11, figs 19–21) specimens are assigned to *Pt. intermedius* on

account of the characteristic pygidial pentagonal M2 (Westergård 1946, 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, here considered questionable, because the distinguishing character of *Pt. atavus*, the absence of the median postaxial furrow, is instead related to ontogeny or to variations within population. *Ptychagnostus atavus coartatus* was erected by Öpik (1979) on the basis of two cephala with the characteristics of *Pt. atavus*. Therefore, both species of Öpik (1979) are here considered synonyms of *Pt. atavus*. Furthermore, Öpik (1979) assigned a complete specimen to *Pt. intermedius* (Tullberg, 1880), although the pygidium shows a hexagonal M2 in outline with a prominent median node; hence, the specimen is better referred to *Pt. atavus*. Egorova *et al.* (1982) figured a subquadrate and not a rounded cephalon, and the characteristic scrobiculation of *Pt. atavus* is not seen in the figure. Rudolph's (1994) single, figured pygidium of *Acidusus atavus* is poorly preserved and its assignment is questionable. He also described the new species *Ac. sterleyi*, which he distinguished from *Pt. atavus* by the lanceolate shape of the pygidial axis and the shaped pygidial F2 furrow by the median pygidial node. These characters are above described as intraspecies variations and *Ac. sterleyi* is thus a synonym of *Pt. atavus*.

Occurrence. *Ptychagnostus atavus* is widespread and was reported from the middle Cambrian lower part of the *Pt. atavus* Zone of Sweden (Öland) and Denmark (Weidner & Nielsen 2009, 2014), the *Pt. atavus* Zone of Utah and Nevada, USA; Mexico, Norway, Sweden, Kazakhstan, Russia (Siberia), Korea and Australia (Öpik 1979; Ergaliev 1980; Egorova *et al.* 1982; Robison 1982; Høyberget & Bruton 2008; Hong & Choi 2015; Ahlberg *et al.* 2016; Wolvers & Maletz 2016; Beresi *et al.* 2017), the upper part of the *Pt. atavus* Zone of Greenland (Robison 1994) and the *Pt. atavus* Zone to the lower part of the *Pt. punctuosus* Zone of China (Peng & Robison 2000). The species is also reported from Newfoundland and Germany, in erratic boulders (Hutchinson 1962; Rudolph 1994; Westrop *et al.* 1996). In the present study *Pt. atavus* occurs in the lower part of the *Pt. atavus* Zone of Eastern Newfoundland.

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 mid-length; median postaxial furrow weakly developed (based on Robison 1994; Shergold & Laurie 1997, with modifications).

Remarks. Tomagnostus fissus, the type species of *Tomagnostus*, was originally described from the Exsulans Limestone Bed of

Brantevik, Scania, Sweden. The systematic position of *Tomagnostus* is still debated. 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) included *Tomagnostus* into his subfamily Tomagnostinae within the 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.

Tomagnostus fissus (Lundgren *in* Linnarsson, 1879)
Figure 11

1879 *Agnostus fissus* Lundgren mscr. *in* Linnarsson, p. 23, pl. 2, fig. 34.
1880 *Agnostus fissus* Lundgr. mscr.; Tullberg, p. 16, pl. 1, fig. 3a–d.
1896 *Agnostus fissus trifissus* 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, pp. 15–16, figs 9–10.
1939 *Tomagnostus (fissus)*; Kobayashi, pp. 152–153, foldout chart in appendix.
1946 *Tomagnostus fissus* (Lundgren MS; Linnarsson); 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); 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); Samson *et al.*, p. 1467, fig. 5C–E.
1990 *Tomagnostus fissus* (Lundgren *in* Linnarsson); Shergold *et al.*, p. 41, fig. 12.6a–b.
1994 *Tomagnostus fissus* (Linnarsson); Robison, pp. 59–60, fig. 30.1–10.
1994 *Tomagnostus fissus* (Lundgren *in* Linnarsson); Rudolph, pp. 127–128, pl. 8 figs 11–13.
1996 *Ptychagnostus (Ptychagnostus) fissus* (Lundgren *in* Linnarsson); Westrop *et al.*, pp. 819–820, fig. 18.1–7.
1997 *Tomagnostus fissus* (Lundgren); Shergold & Laurie, p. 354, fig. 224.3a–b.
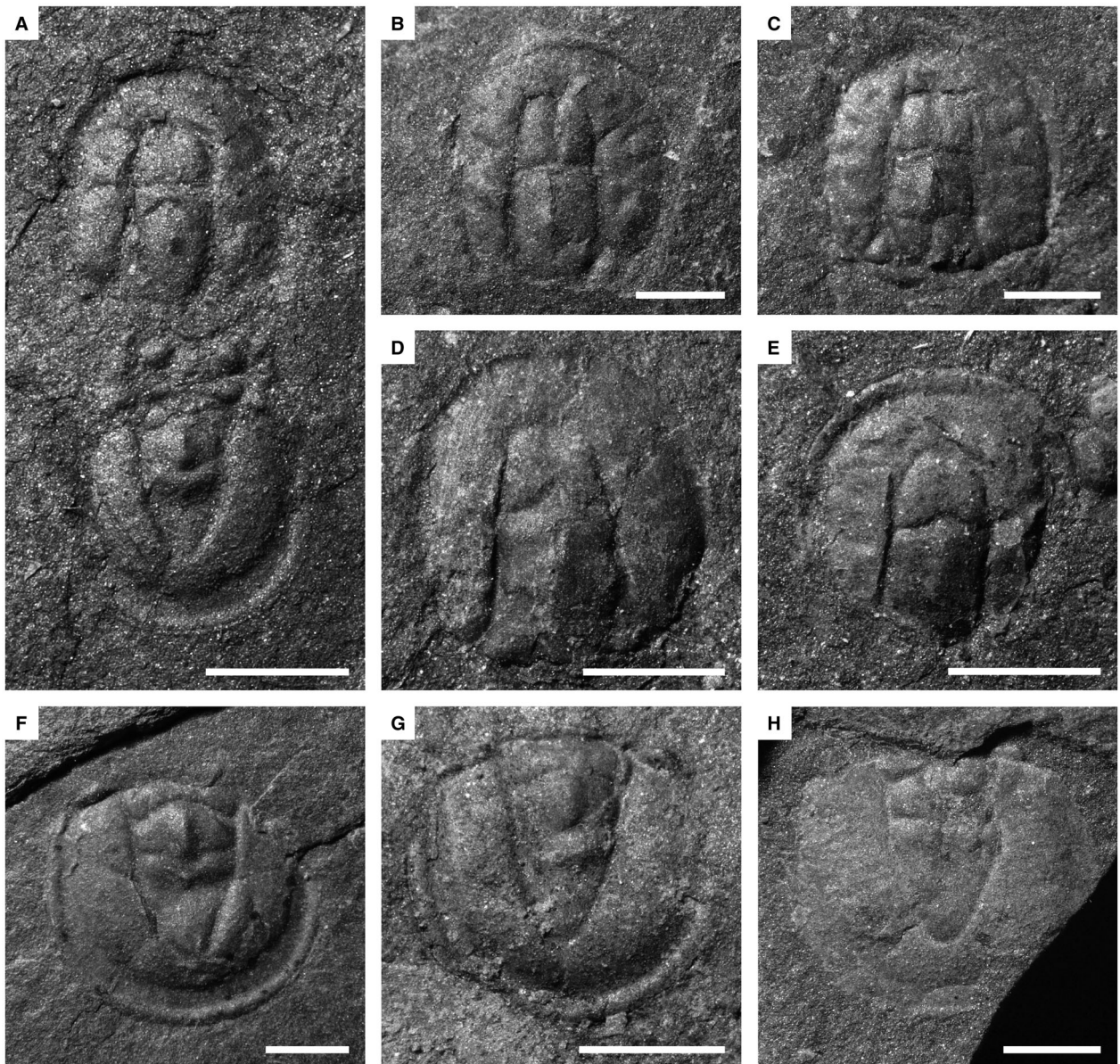
FIG. 11. *Tomagnostus fissus* (Lundgren *in* Linnarsson, 1879). A, complete specimen (NFM F-1709). B, cephalon (NFM F-1652). C, cephalon (NFM F-1651). D, cephalon (NFM F-1719). E, cephalon (NFM F-1703). F, pygidium (NFM F-1653). G, pygidium (NFM F-1665). H, pygidium (NFM F-1712). Scale bars represent 1 mm.

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

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

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

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

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

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

2014 *Tomagnostus fissus* (Linnarsson); Rees *et al.*, pp. 8–9, fig. 1.5f.

2014 *Tomagnostus fissus* (Lundgren *in* Linnarsson); Weidner & Nielsen, pp. 43–44, fig. 19A–D.

2015 *T. fissus* (Lundgren *in* Linnarsson, 1879); Weidner & Nielsen, p. 18, fig. 11A–J.

2016 *Tomagnostus fissus* (Lungren); Korovnikov & Shabanov, pp. 570–571, pl. 2, fig. 17.

Neotype. SGU 4840, by subsequent designation of Westergård (1946, p. 58, pl. 7, fig. 22), refigured by Shergold & Laurie (1997, fig. 224: 3a). According to Westergård (1946), the holotype is lost.

Material. 2 complete specimens, 56 cephala and 23 pygidia (NFM F-1651–F-1731) from the lower part (3.89–7.70 m) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

Diagnosis. Moderately scrobiculate genae; anterior glabellar lobe with frontal sulcus variable prolonging into preglabellar field; elongate cephalic 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 (based on Westrop *et al.* 1996; Høyberget & Bruton 2008, with modifications).

Description. The specimens are poorly to well-preserved. The complete specimens are 4 mm and 7.9 mm long, respectively. The cephala vary in size from 0.9 to 4.1 mm in width and from 1.1 to 3.9 mm in length, and the pygidia vary in size from 2.0 to 3.1 mm in width and from 2.0 to 2.9 mm in length. Some of the specimens have 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. Larger specimens have moderately developed scrobicules, some with a well-developed frontal sulcus, which may extend into the preglabellar 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.

Remarks. This species is easily distinguished from closely related species by its subelliptical to subquadrate cephalon and pygidium (Westergård 1946; Weidner & Nielsen 2014). The anterior glabellar lobe has a frontal sulcus developed, which often extends into the preglabellar field. Another characteristic feature is the strongly anteriorly curved glabellar F3 furrow (Høyberget & 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 & Nielsen 2014). Both species show a depressed pygidial posteroaxis, but *T. perrugatus* also has a pair of pygidial posterolateral spines.

Linnarsson (1879) erected *Tomagnostus fissus* and described the characteristic scrobiculation on the cephalic genae. In his view, the scrobiculation on his specimens at hand was too faint, therefore he figured the cephalon as 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 intraspecies variation. An example of the different cephalic scrobicules is shown by Robison (1994). In the synonymy list of Rudolph (1994), *Agnostus fissus* of Matthew (1896, pl. 16, fig. 10) was listed. This was actually a figure of the subspecies *Agnostus fissus* var. *trifissus*. Samson *et al.* (1990) figured a poorly preserved cephalon and two pygidia, which are here included into *T. fissus* with doubts. Rudolph (1994) listed *Triplagnostus fissus* of Shergold *et al.* (1990) in his synonymy list, although that 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 accepted a wide morphological variability within *T. fissus*. The figured cephalon of Laurie (2008) does not show characteristics of *T. fissus*, that is, the cephalon has no scrobicules, the frontal sulcus is small and faint and the glabellar F3 furrow is not curved anteriorly; the assignment to *T. fissus* is here considered questionable.

Occurrence. Tomagnostus fissus was reported globally from the middle Cambrian *Pt. gibbus* Zone to the upper part of the *Pt. atavus* Zone (Høyberget & Bruton 2008; Weidner & Nielsen 2014). It is also reported from the *Pt. gibbus* Zone of Germany, in erratic boulders (Rudolph 1994), the *Triplagnostus gibbus* Zone to the *Ac. atavus* Zone of Sweden (Weidner & Nielsen 2015), the upper part of the *Pt. gibbus* Zone to the lower part of the *Pt. atavus* Zone of Sweden and Greenland (Westergård 1946; Robison 1994), the lower part of the *Pt. atavus* Zone of Denmark and Siberia (Pegel 2000; Weidner & Nielsen 2014), the *Pt. atavus* Zone of North and South Carolina, USA, Norway, England, and Western Newfoundland (Kindle 1982; Illing 1915; Samson *et al.* 1990; Høyberget & Bruton 2008) and the *T. fissus* Zone of Wales and Siberia (Rees *et al.* 2014; Korovnikov & Shabanov 2016). The species was also reported from New Brunswick, Japan and Australia (Howell 1935; Kobayashi 1939; Shergold *et al.* 1990). In the present study *T. fissus* occurs at the lower part of the *T. fissus* Zone of Eastern Newfoundland.

Tomagnostus perrugatus (Grönwall, 1902)
Figures 12, 13

1902   *Agnostus fissus* Lgn. MS., var. *perrugata* Grönwall,   p. 50, pl. 1, fig. 1.
? 1915   *Agnostus fissus*, var. *perrugatus* Grönwall; Illing,   p. 407, pl. 28, fig. 9.
1915   *Agnostus sulcatus* Illing, pp. 411–412, pl. 30,   figs 3–6.
1946   *Tomagnostus perrugatus* (Grönwall); 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); Rushton,   pp. 55–56, fig. 6C–E.
1981   *Tomagnostus renata* Fatka *et al.*, pp. 368–369, pl. 2,   figs 3–5.
1982   *Tomagnostus perrugatus* (Grönwall); Egorova *et al.*,   p. 59, pl. 17, figs 5–6; pl. 54, figs 9, 12.
1982   *Tomagnostus deformis* Pokrovskaya; Egorova *et al.*,   p. 60 (pars), pl. 5 fig. 5 (non pl. 8, fig. 9; pl. 12, fig. 13).
1988   *Tomagnostus perrugatus* (Grönwall); Martin &   Dean, p. 17, pl. 3, fig. 2.
1992   *Tomagnostus* cf. *perrugatus* (Grönwall); Fatka &   Kordule, p. 60, pl. 2, fig. 3.
1994   *Tomagnostus perrugatus* (Grönwall); Robison, p. 60,   fig. 31.1–3.
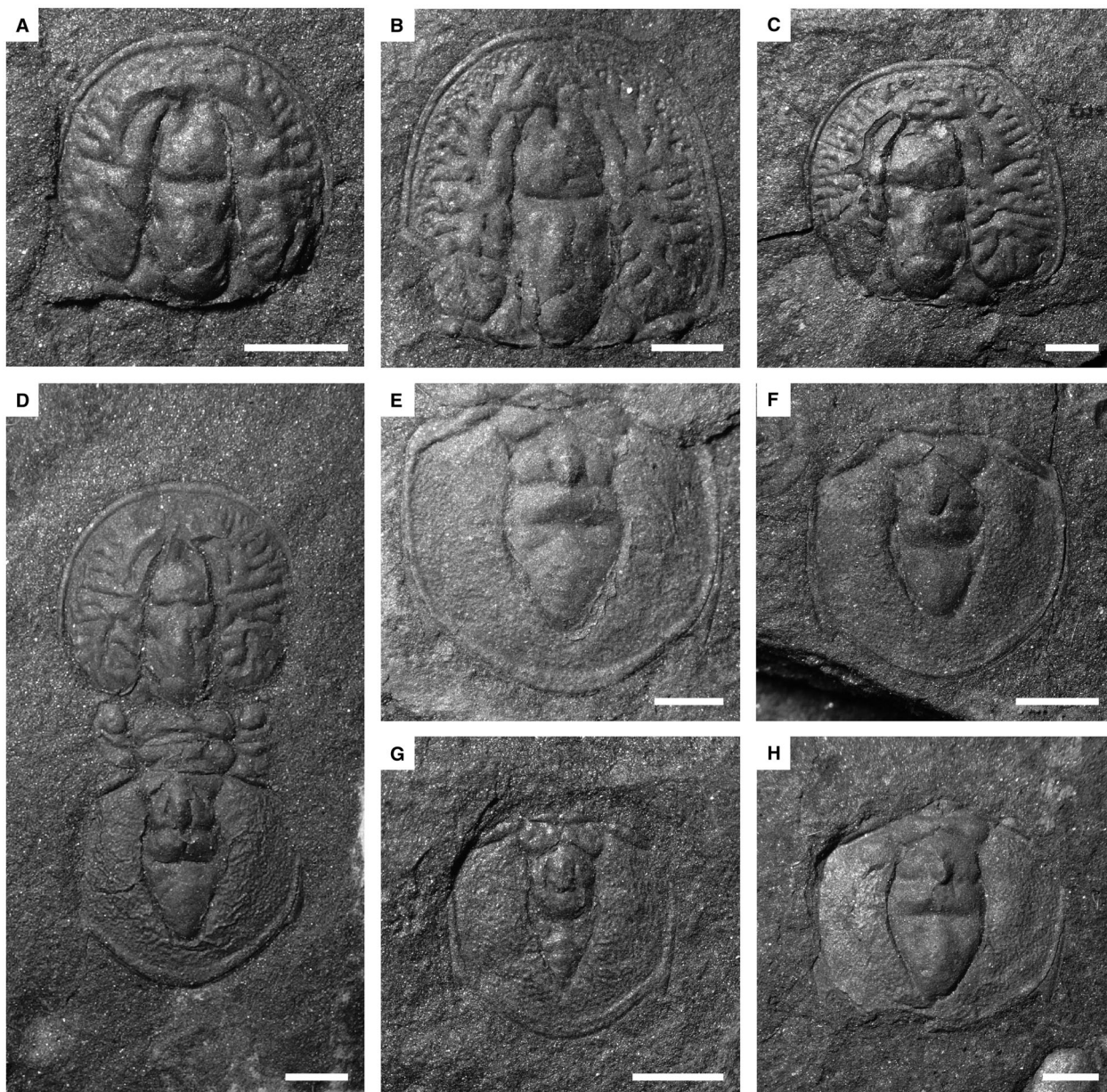1994   *Tomagnostus perrugatus* (Grönwall); Rudolph,   pp. 128–129, pl. 8, fig. 14.

FIG. 12. *Tomagnostus perrugatus* (Grönwall, 1902). A, cephalon (NFM F-1793). B, cephalon (NFM F-1733). C, cephalon (NFM F-1801). D, complete specimen (NFM F-1732). E, pygidium (NFM F-1734). F, pygidium (NFM F-1794). G, pygidium (NFM F-1819). H, pygidium (NFM F-1873). Scale bars represent 1 mm.

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

2014 *Tomagnostus perrugatus* (Grönwall); Rees *et al.*, p. 16, fig. 1.9c–d.

2014 *Tomagnostus perrugatus* (Grönwall); Weidner & Nielsen, pp. 44–45, fig. 20A–F.

2015 *T. perrugatus* (Grönwall); Weidner & Nielsen, p. 18, fig. 11K–T.

2016 *Tomagnostus perrugatus* (Grönwall); Weidner & Nielsen, pp. 114–115, fig. 3E–H.

2017 *Tomagnostus deformis* Pokrovskaya; Naimark & Pegel, pp. 1180–1181, pl. 1, fig. 4.

Holotype. MGUH 143, by original designation of Grönwall (1902, p. 50, pl. 1, fig. 1) and refigured by Weidner & Nielsen (2014, p. 22, fig. 20A).

Material. 21 complete specimens, 105 cephala and 89 pygidia (NFM F-1732–F-1946) from the interval 2.73–14.97 m of the
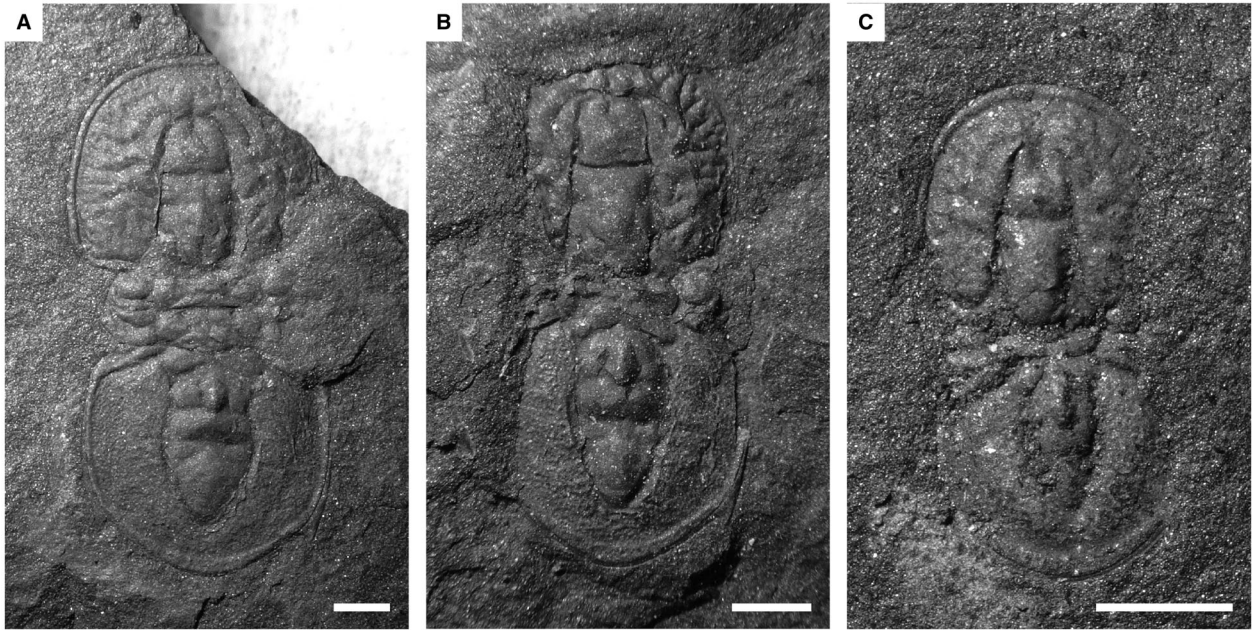
FIG. 13. *Tomagnostus perrugatus* (Grönwall, 1902). A, complete specimen (NFM F-1863). B, complete specimen (NFM F-1779). C, complete specimen (NFM F-1843). Scale bars represent 1 mm.

Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

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).

Description. The specimens are well-preserved. The complete specimens vary from 4.3 to 11.0 mm in length. The cephala vary in size from 2.1 to 4.9 mm in width and from 2.1 to 5.4 mm in length, and the pygidia vary in size from 2.0 to 6.2 mm in width and from 2.2 to 6.3 mm 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 the preglabellar field as a median preglabellar furrow. Larger specimens show characteristic 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.

Remarks. This species is easily distinguished from the closely related *T. fissus* by rounded cephala and pygidia, strong scrobiculate cephalic genae, a crescentic pair of furrows opposite the anterior glabellar lobe, small pits on the pygidial pleural fields and small pygidial posterolateral spines (Weidner & Nielsen 2014). Westergård (1946) and Rushton (1979) described differences in pygidia shape depending on the stratigraphic horizon. According

to Westergård (1946), specimens from earlier zones have a pygidial collar on the posterior border between the pair of posterolateral spines. Specimens from stratigraphically younger horizons have 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 some specimens with the pygidial collar. In an emended diagnosis, Robison (1994) suggested that the specimens are without or with a pygidial collar. Robison (1994, fig. 31.2–3) showed pygidia with a curved to tapered margin in between the posterolateral spines. Specimens from Newfoundland show the curved to tapered margin without pygidial collars. The pygidial collar seems to be an intraspecies variation of *Tomagnostus perrugatus*.

Grönwall (1902) described and figured a 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, here tentatively assigned to *T. perrugatus*. The figure is not clear enough to show if a crescentic pair of furrows is developed. Illing (1915) erected the species *Agnostus sulcatus*. His four complete specimens show typical characters of *T. perrugatus* such as cephalic scrobiculate genae, the frontal sulcus and the crescentic pair of furrows next to the anterior glabellar lobe. Their pygidia have the characteristic rounded to pentagonal margin with a broad border, pits on the pleural fields and a pair of posterolateral spines. The poorly preserved specimen of Illing (1915) might show a pygidial collar. *Agnostus sulcatus* is thus here suggested to be a synonym of *T. perrugatus*. Fatka *et al.* (1981) assigned their three figured cephala to the species *Tomagnostus renata*. The figures and the description agree well with *T. perrugatus*. According to Fatka *et al.* (1981), the main distinguishing characters are different scrobicules on the cephalon, which are not

visible on the figures. These specimens are here assigned to *T. perrugatus*. Egorova *et al.* (1982) described *Tomagnostus deformis* and figured three specimens, among them a complete specimen (Egorova *et al.* 1982, pl. 5, fig. 5) that has all the characteristics of *T. perrugatus*. The two other specimens are too poorly preserved for determination. Naimark & Pegel (2017) illustrated a complete specimen with specific characters of *T. perrugatus*.

Occurrence. *Tomagnostus perrugatus* is widespread and was observed from the middle Cambrian *Pt. gibbus* to the *Pt. punctuosus* Zone (Rushton 1979; Robison 1994). It has been reported in the *Pt. gibbus* Zone of Germany, in erratic boulders (Rudolph 1994), the *Pt. gibbus* to the *Pt. atavus* Zone of England, Sweden and the Czech Republic (Westergård 1946; Rushton 1979; Fatka & Kordule 1992), the *Triplagnostus gibbus* Zone to the *Ac. atavus* Zone of Sweden (Weidner & Nielsen 2015, 2016), the *T. fissus* Zone to the *H. parvifrons* Zone of Wales (Rees *et al.* 2014), the *T. fissus* Zone to the *Anopolenus henrici* Zone of Siberia (Naimark & Pegel 2017) and the *Pt. atavus* Zone of Newfoundland, Canada, Greenland, Denmark and Russia (Siberia) (Hutchinson 1962; Egorova *et al.* 1982; Robison 1994; Weidner & Nielsen 2014; Naimark & Pegel 2017). In the present study *T. perrugatus* ranges from the *T. fissus* Zone to the *Pt. atavus* Zone of Eastern Newfoundland.

Family CONDYLOPYGIDAE Raymond, 1913

Genus PLEUROCTENIUM Hawle & 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; Shergold & Laurie 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 main characters that differentiate Condylopygoidea from Agnostoidea are the expansion of the anterior glabellar lobe, the absence of basal lobes and the presence of three segments in the pygidial anteroaxis. In addition, the Condylopygoidea are characterized by their variable spines on cephala and pygidia, described by Rushton (1966, 1979). The superfamily contains a single family Condylopygidae and two genera, *Condylopyge* and *Pleuroctenium* (Shergold *et al.* 1990). *Pleuroctenium* is 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. In contrast, *Condylopyge* also has 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)
Figure 14

1846 *Battus granulatus* Barrande, pp. 15–16.
1847 *Pleuroctenium granulatum*, nob.; Hawle & Corda, pp. 116–117, pl. 6, fig. 63.
1852 *Agnostus granulatus* Barrande; Barrande, p. 911, pl. 49, figs 1a–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)*; Kobayashi, pp. 109–110, fold-out chart in appendix.
1946 *Pleuroctenium scanense* Westergård, pp. 35–36, pl. 2, figs 14–17.
1958 *Pleuroctenium granulatum* (Barrande); Šnajdr, pp. 56–59 (pars), pl. 2, figs 5, 7–13 (non figs 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 10a–14.
? 1963 *Pleuroctenium granulatum* (Barrande); Smith & White, pp. 400–401, pl. 57, figs 5–9.
1966 *Pleuroctenium granulatum granulatum* (Barrande); Rushton, pp. 32–33, text-fig. 13b.
1966 *Pleuroctenium granulatum scanense* Westergård; Rushton, pp. 32–33, text-fig. 13c.
non 1966 *Pleuroctenium granulatum pileatum* Rushton, pp. 32–33, text-fig. 13a, pl. 4, figs 18–24.
1970 *Pleuroctenium granulatum* (Barrande); Horný & Bastl, pl. 1, fig. 6.
? 1979 *Pleuroctenium granulatum granulatum* (Barrande); Rushton, pp. 46–47, fig. 2A–B.
1979 *Pleuroctenium granulatum scanense* Westergaard; Rushton, pp. 47–48, fig. 2J–K.
1990 *Pleuroctenium granulatum granulatum* (Barrande); Shergold *et al.*, pp. 92–93, fig. 19.3a.
1990 *Pleuroctenium granulatum* (Barrande) *scanense* Westergård, 1946; Shergold *et al.*, pp. 92–93, fig. 19.3b.
1997 *Pleuroctenium granulatum scanense*; Shergold & Laurie, pp. 382, fig. 240.4a.
1997 *Pleuroctenium granulatum* (Barrande); Shergold & Laurie, pp. 382, fig. 240.4b.
2004 *Pleuroctenium granulatum granulatum* (Barrande); Fatka *et al.*, p. 77, pl. 1, fig. 1, text-fig. 2.
2006 *Pleuroctenium granulatum scanense* Westergård; Fletcher, pp. 66–67, pl. 34, figs 45–46.

Lectotype. ČC 250 NMP 1008, by subsequent designation of Šnajdr (1958, pl. 2, fig. 5), originally illustrated by Barrande (1852, pl. 49, figs 5–7).
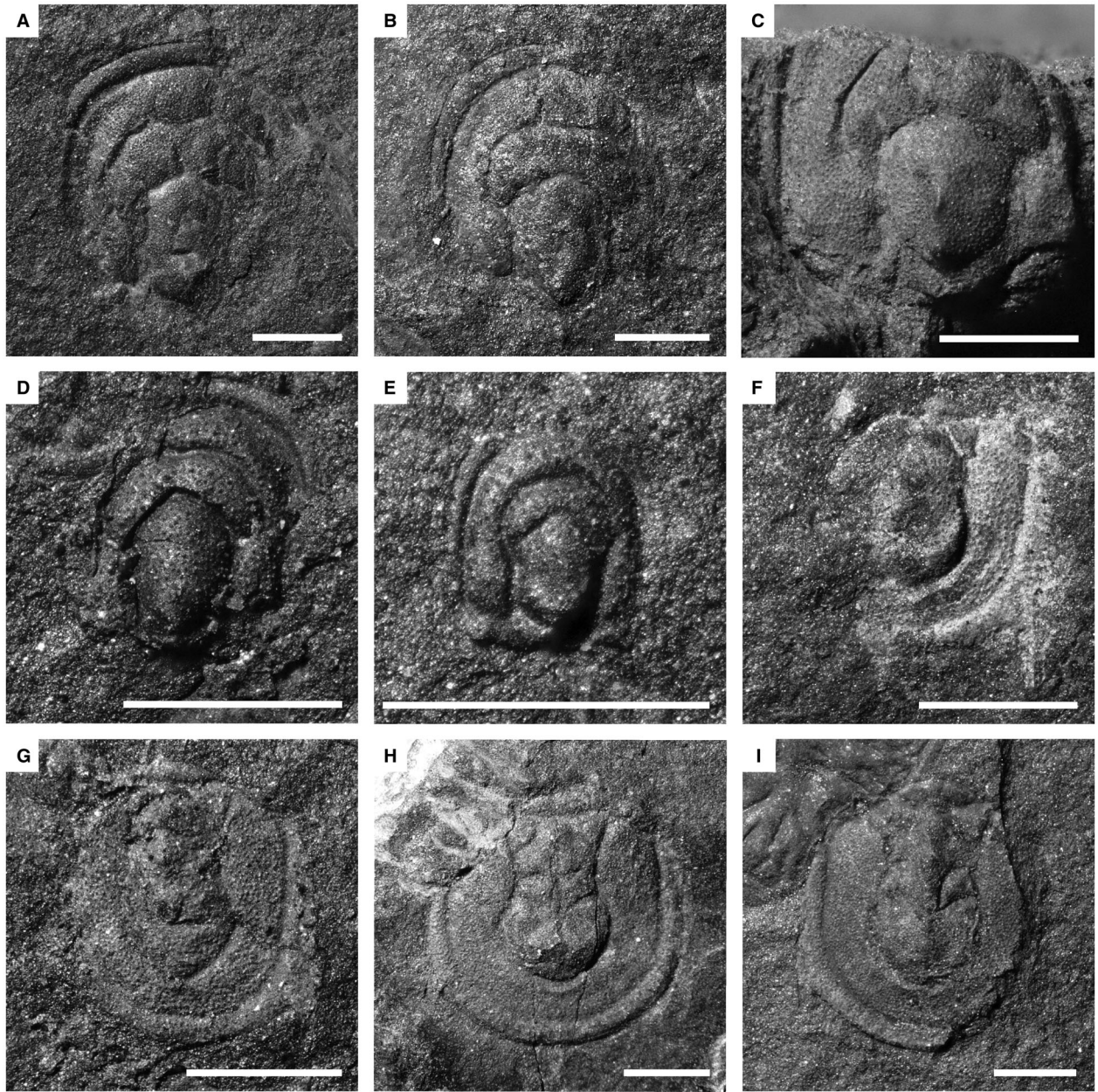
FIG. 14. *Pleuroctenium granulatum* (Barrande, 1846). A, cephalon (NFM F-1966). B, cephalon (NFM F-1947). C, cephalon (NFM F-1949). D, cephalon (NFM F-1957). E, cephalon (NFM F-1958). F, pygidium (NFM F-1950). G, pygidium (NFM F-1959). H, pygidium (NFM F-1948). I, pygidium (NFM F-1964). Scale bars represent 1 mm.

Material. 20 cephala and 9 pygidia (NFM F-1947–F-1975) from almost the entire Manuels River Formation (2.12–15.43 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.

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

Description. Most specimens are poorly preserved and fragmentary. The cephala vary in size from 0.6 to 2.6 mm in width and from 0.7 to 2.8 mm in length, and the pygidia vary in size 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. In 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 of the posterior glabellar lobe is situated at the rearmost posterior part of the lobe. The cephalic and pygidial borders are narrow. All pygidia have a broad and rounded axis with three pairs of lateral furrows and nodes. The lateral borders of the pygidia are serrated. One fragmentary pygidium has a long posterolateral spine, all other pygidia have short spines, which might be an intraspecies variation. In addition, all cephala and pygidia show a granular surface.

Remarks. Pleuroctenium granulatum shows strong morphological variations within populations (Rushton 1966, 1979). The anterior glabellar lobe is in some specimens rounded anteriorly and truncated in other specimens. The rounded anterior lobe is interrupted by a frontal sulcus. Other specimens have a median lateral furrow through the lobe that is variable in depth (Rushton 1966). Also, a small spine next to the axial node and posterolateral cephalic spines vary in development or are absent. A pair of pygidial posterolateral spines is always present and the spines vary in length. Fatka *et al.* (2004) described the serrated lateral margin of the pygidia and the spines. Between *c.* 22 and 30 small spines occur on each side of the margin. The closely related species *Pl. bifurcatum* differs from *Pl. 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 *Pl. bifurcatum* is slender, in contrast to the broad axis of *Pl. granulatum*. Neither the lateral border, nor the spines are serrated in *Pl. bifurcatum*. *Pleuroctenium tuberculatum* is distinguished from *Pl. granulatum* by a very small anterior glabellar lobe, which is rounded anteriorly. The posterior glabellar lobe of *Pl. tuberculatum* is ovate and slender. The pygidial posteroaxis is shorter than that of *Pl. granulatum* (Rushton 1966). In addition, the lateral serration of the pygidial border and spines is absent in *Pl. tuberculatum*.

Hawle & Corda (1847) described the new genus *Pleuroctenium* to which they assigned the species *Pl. granulatum*. Jaekel (1909) described the new genus *Dichagnostus* on the basis of such characters as a large anterior glabellar lobe with furrow, a broad tripartite pygidial axis and pygidial spines. In addition, Jaekel's (1909) illustration of *Pl. granulatum* shows a serrated lateral margin of the pygidia and the spines, it is here assigned to *Pl. granulatum*. Westergård (1946) erected the species *Pl. scanense* on the basis of two cephala and four pygidia. He remarked that the specimens were too poorly preserved for a detailed description but concluded that this species is distinguished from *Pl. granulatum* by a deeper frontal sulcus of the anterior glabellar lobe, a slender pygidial posteroaxis and a shorter pair of pygidial posterolateral spines. In contrast, the figured specimens show the typical characters of *Pl. granulatum*, here suggested to be intraspecies variations. *Pleuroctenium scanense* is here considered a synonym of *Pl. granulatum*. The specimen of Šnajdr (1958) consists only of fragments in poor preservation, so an assignment to this species is suggested to be doubtful. A complete specimen of Šnajdr (1958) shows an anteriorly rounded anterior glabellar lobe, cephalic spines and a slender pygidial axis, characters that are typical of *Pl. bifurcatum*. Hutchinson (1962) misspelled the genus *Pleurectinium*

and provided no description. The figured specimens of Smith & White (1963) are poorly preserved and the assignment to *Pl. granulatum* is considered questionable. Because of the wide intraspecies variations of *Pl. granulatum* the concept of Rushton (1966) to divide the species into three subspecies was followed by several authors. Rushton (1966) characterized *Pl. 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 *Pl. granulatum scanense* of Rushton (1966), which was first described by Westergård (1946), was characterized by a frontal sulcus visible at the anterior glabellar lobe, short pygidial posterolateral spines, and serration at the lateral pygidial margin. Later, Rushton (1979), Shergold *et al.* (1990), Shergold & Laurie (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 intraspecies variations. The third subspecies of Rushton (1966), *Pl. granulatum pileatum*, was characterized 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 *Pl. bifurcatum*.

Occurrence. Pleuroctenium granulatum was reported from the middle Cambrian *Pt. atavus* Zone of Newfoundland, England and the Czech Republic (Šnajdr 1958; Hutchinson 1962; Smith & White 1963; Rushton 1966, 1979), and the upper part of the *Pt. atavus* Zone of Sweden (Westergård 1946). The species is also reported from Japan and Australia (Kobayashi 1939; Shergold *et al.* 1990). In the present study *Pl. granulatum* ranges from the *T. fissus* Zone to the *Pt. atavus* Zone of Eastern Newfoundland.

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, 1883.

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, 1864; *Spinodiscus* Kobayashi, 1943; *Deltadiscus* Kobayashi, 1943.

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

easily 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 crenulate 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). The systematic position of eodiscid trilobites is still under discussion. Babcock (1994) classified Eodiscidae as doubtful because of the phylogenetic status. Axheimer & Ahlberg (2003) classified the order as uncertain without any remarks. The order Agnostida is originally 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). The concept to assign all genera of Eodiscidae to the Agnostida, is here followed.

Eodiscus punctatus (Salter, 1864)
Figure 15

1864 *Microdiscus punctatus* Salter, pp. 237–238, pl. 13, fig. 11a–c.

1883 *Microdiscus eucentrus* Linnarsson, pp. 30–31, pl. 4, figs 19–20.

1884 *Microdiscus punctatus*, Salter; Walcott, pp. 24–25 (pars), pl. 2, fig. 1c (non fig. 1–1b).

? 1886 *Microdiscus punctatus*, var. *precursor* Matthew, p. 75, pl. 7, fig. 13.

non 1886 *Microdiscus punctatus* (Salter), var. *pulchellus*, Hartt; Matthew, pp. 74–75, pl. 7, fig. 12a–c.

1907 *Microdiscus punctatus*, Salter; Lake, pp. 36–39 (pars), pl. 3, figs 11–15 (non figs 16–17a).

1911 *Microdiscus* sp., cf. *M. punctatus* Salt.; Cobbold, p. 292, pl. 25, fig. 12a–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 11a–12.

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

1946 *Eodiscus punctatus* (Salter); 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, fig. 129.1a–b.

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

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

1969 *Eodiscus punctatus* (Salter); Poulsen, p. 3 (pars), fig. 2B (non fig. 2A).

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

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

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

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

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

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

? 2014 *Eodiscus punctatus scanicus* (Linnarsson); Rees *et al.*, pp. 8–9, fig. 1.9f, i, k–m.

2014 *Eodiscus punctatus punctatus* (Salter); Rees *et al.*, pp. 16, fig. 1.9 g–i.

? 2014 *Eodiscus punctatus* (Salter); Weidner & Nielsen, pp. 67–68, fig. 40A–I.

Lectotype. BMNH 42646, by subsequent designation of Morris (1988, p. 91), originally figured by Salter (1864).

Material. 2 complete specimens, 215 cephala and 213 pygidia (NFM F-1976–F-2405) from the interval 2.24–16.67 m of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

Diagnosis. Deep median preglabellar furrow; wide cephalic border; cephalic genae and pygidial pleural fields convex; long occipital cephalic spine; pygidial axis segmented in 7–9 rings.

Description. The specimens are mainly well-preserved. The complete specimens, preserved as moulds, are 7.8 and 8.8 mm long, respectively. The cephala vary in size from 2.2 to 3.9 mm in width and from 1.6 to 3.6 mm in length, and the pygidia vary in size from 2.2 to 4.2 mm in width and from 1.9 to 3.9 mm in length. Some specimens have a yellow surface from the containing pyrite in the shales. The cephala and pygidia have a semiovate shape, rather broad than long. Cephala are mainly tapered anteriorly, in some cases they are more rounded. The cephalic border shows fine radiating furrows, often better preserved in moulds than on body fossils. All specimens have deep median preglabellar furrows and glabellar furrows. The cephalic occipital spine is in most specimens long, in others the spine is broken, probably a matter of preservation. The surface of the cephalic genae and the pygidial pleural fields varies from nearly smooth to strongly punctate, with the strongest punctation often on larger specimens. All specimens have a characteristic convex shape of genae and pleural fields. The pygidial axis has deep axial furrows and seven to, mainly, nine rings.

Remarks. Eodiscus punctatus shows a wide range of intraspecies morphological variations throughout ontogeny (Lake 1907;
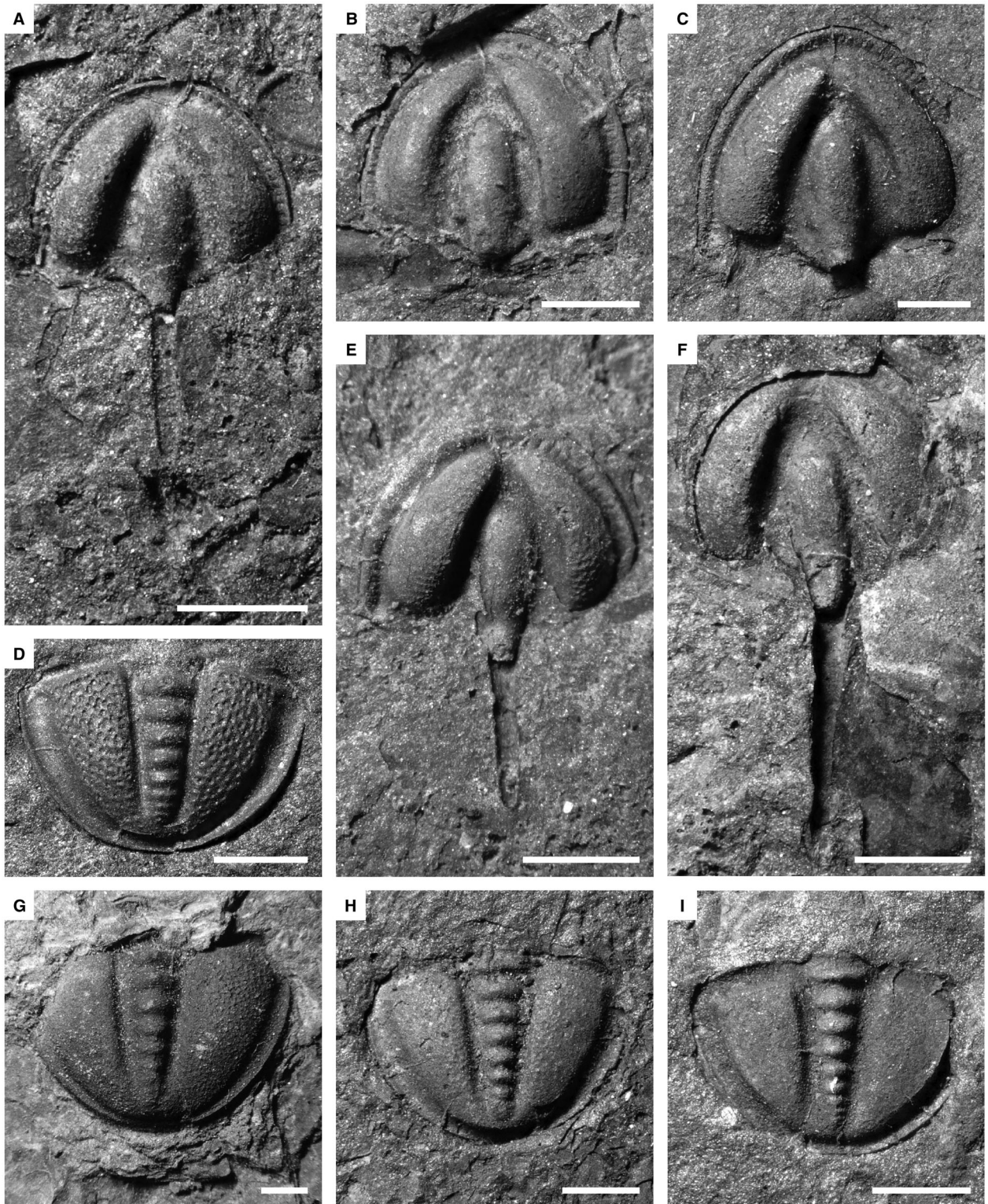
FIG. 15. *Eodiscus punctatus* (Salter 1864). A, cephalon (NFM F-2349). B, cephalon (NFM F-2383). C, cephalon (NFM F-1977). D, pygidium (NFM F-1978). E, cephalon (NFM F-1976). F, cephalon (NFM F-2350). G, pygidium (NFM F-2022). H, pygidium (NFM F-2123). I, pygidium (NFM F-2124). Scale bars represent 1 mm.

Westergård 1946; Rasetti 1952; Høyberget & Bruton 2008; Weidner & Nielsen 2014). The fine radiating furrows on the cephalic borders vary from very faint to well-developed. The surface ornamentation of the cephala and pygidia varies from smooth punctate to strongly punctate and is an inappropriate characteristic for species determination (Westergård 1946; Rasetti 1952). It also varies during different ontogenetic stages from fainter in the meraspis stage to stronger in the holaspis stage.

The occipital spine is in some specimens longer, in others shorter. In addition, the angle of the spine varies from 20° to 45° (Westergård 1946; Weidner & Nielsen 2014). Because of the length, the slenderness and the angle, the spine is preserved broken in some specimens. In the past only the length and the angle of the spine were used to distinguish *E. punctatus* from *E. scanicus* (Rasetti 1952; Hutchinson 1962; Poulsen 1969), but it is rarely preserved and thus is a challenging characteristic. Other characters can be used for distinguishing *E. punctatus* and *E. scanicus*, such as 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 the pygidial pleural fields, and the number of pygidial axial rings, which range from seven to nine segments. In contrast, *E. scanicus* has 10 or more pygidial axial rings (Rasetti 1952; Høyberget & Bruton 2008; Weidner & Nielsen 2014). Linnarsson (1883) described the species *Microdiscus eucentrus*. He figured a cephalon and a pygidium, which both have 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, both typical for *E. punctatus*, thus the species *M. eucentrus* is here considered a synonym of *E. punctatus* (cf. Høyberget & Bruton 2008).

Walcott (1884) figured three cephala and a single pygidium of *Microdiscus punctatus*. The pygidium shows the characteristics 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, a broad glabella without an occipital spine and broad and deep median preglabellar furrow and axial furrows. In the absence of an illustrated pygidium for the subspecies, the assignment to *E. punctatus* is here considered questionable. Furthermore, Matthew (1886) described 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, an occipital spine as long as the glabella, and a narrow pygidial axis segmented by 11 rings. Therefore, this subspecies is included into *E. scanicus*. Lake (1907) illustrated two complete specimens and four cephala assigned to *M. punctatus*, which all match well with *E. punctatus*. Further, he figured three pygidia with a long and narrow pygidial axis segmented by 10 rings. The pygidial pleural fields are not as convex as those of *E. punctatus* and one of the pygidia has a smooth surface. The figured pygidia of Lake (1907, figs 16–17a) are here assigned to *E. scanicus*. Cobbold (1911) collected scattered pygidia uncertain about the assignment to

E. punctatus. The illustrated pygidia show the typical characteristics of *E. punctatus* such as a long narrow pygidial axis with seven ring segments. Raymond (1913) illustrated a complete specimen assigned *E. punctatus* with 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) specimen is here excluded from *E. punctatus*. Illing (1915) figured three complete specimens assigned to the subspecies *M. punctatus scanicus*. They all show a faint median preglabellar furrow and 11 rings on the pygidial axis, typical for *E. scanicus*. Kobayashi (1944) figured a complete specimen and erected the genus *Spinodiscus*. He assigned *M. punctatus* as the type species of the new genus. *Spinodiscus* is here considered a synonym of *Eodiscus* (see above). Hutchinson (1962) illustrated three cephala and pygidia under *E. scanicus*. These specimens have exactly the same characters as his figures of *E. punctatus* and he stated that the two species are very similar and they show intermediate forms. His specimens of *E. scanicus* are here included into *E. punctatus*. Poulsen (1969) figured a cephalon and a pygidium. The pygidium agrees well with *E. punctatus* but the cephalon shows a faint median preglabellar furrow and the genae are flat. Thus, the cephalon (Poulsen, 1969, fig. 2a) is here not assigned to this species. Egorova *et al.* (1982) figured several specimens. Two cephala have 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 from Kindle (1982) show the typical characteristics of *E. scanicus* such as a faint median preglabellar furrow, a short occipital spine, 11 pygidial axial rings and a smooth surface. Martin & Dean (1988) figured two cephala and one pygidium, with typical characters of *E. punctatus*, therefore they are here assigned to this species (cf. Høyberget & Bruton 2008). Fletcher (2006) figured an overview of several specimens on a rock slab with a resolution that was not appropriate for the determination of any species. Therefore, an assignment to *E. punctatus* is here considered doubtful. Rees *et al.* (2014) illustrated one complete specimen and three cephala. All cephala have a faint to moderate median preglabellar furrow, which is typical for *E. scanicus*. The complete specimen shows eight pygidial axial rings and convex cephalic genae and pygidial pleural fields. These characters are typical for *E. punctatus*. Only the deep median preglabellar furrow is absent. This is a morphological intraspecies variation or a variation throughout ontogeny, hence an assignment to this species is here suggested to be questionable. Weidner & Nielsen (2014) figured six cephala and three pygidia. Almost all specimens have the typical characteristics of *E. punctatus* and therefore match well with the species. In contrast, all cephala have a faint median preglabellar furrow, typical of *E. scanicus*. Thus, the assignment to *E. punctatus* is here suggested to be questionable.

Occurrence. Eodiscus punctatus is widespread and has been reported from the middle Cambrian lower part of the *Pt. atavus* Zone of Siberia (Egorova *et al.* 1982), the *Pt. atavus* Zone of New Brunswick and Nova Scotia, Canada, and Greenland (Hutchinson 1952; Poulsen 1969), the upper part of the *Pt. atavus* Zone of Wales and England (Matthew 1886; Illing 1915), the upper *H. parvifrons* Zone of Wales (Rees *et al.* 2014), the upper part of

the *Pt. atavus* Zone to the lower part of the *Pt. punctuosus* Zone of Newfoundland, Denmark and Sweden (Grönwall 1902; Westergård 1946; Hutchinson 1962; Fletcher 2006; Weidner & Nielsen 2014), and the *Pt. punctuosus* Zone of Germany, in erratic boulders, and Norway (Rudolph 1994; Høyberget & Bruton 2008). The species is also reported from Japan (Kobayashi 1944). In the present study *E. punctatus* ranges from the *T. fissus* Zone to the *Pt. atavus* Zone of Eastern Newfoundland.

Author contributions. The study is based on fieldwork by AH and GA in 2012 and 2013 and parts of AH's PhD thesis at Heidelberg University, Germany (Hildenbrand 2016). Palaeontological interpretations and implications were developed from discussions with GA, PB and CI. The manuscript was prepared with input from all co-authors.

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