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Tanja UNGER, Anne HILDENBRAND,
Wolfgang STINNESBECK & Gregor AUSTERMANN



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Biostratigraphy and taxonomy of polymerid trilobites of the Manuels River Formation (Drumian, middle Cambrian), Newfoundland, Canada

Tanja UNGER

Institut für Geowissenschaften, Universität Heidelberg,
Im Neuenheimer Feld 234, 69120 Heidelberg (Germany)
and Institut für Geologie, Mineralogie und Geophysik,
Ruhr-Universität Bochum, 44801 Bochum (Germany)
tanja.unger@ruhr-uni-bochum.de

Anne HILDENBRAND
Wolfgang STINNESBECK
Gregor AUSTERMANN

Institut für Geowissenschaften, Universität Heidelberg,
Im Neuenheimer Feld 234, 69120 Heidelberg (Germany)

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ABSTRACT

Newfoundland's middle Cambrian fine-clastic Manuels River Formation is renowned for its well-preserved trilobite fauna. Here we present a newly collected assemblage of 1184 specimens from the type locality at Conception Bay South, Newfoundland, Canada. The faunal assemblage comprises detailed information about the accurate ranges of each species. Thus, the polymerid *Paradoxides davidis* and *Paradoxides hicksi* zones previously established for the region and the globally recognised agnostid *Tomagnostus fissus*, *Hypagnostus parvifrons*, *Ptychagnostus atavus*, and *Ptychagnostus punctuosus* zones are now precisely correlated. The polymerid fauna is comparable with that of other regions of Avalonia, Baltica, and partly with Gondwana. Our analysis of the faunal assemblage demonstrates that there is a need for comprehensive revisions of Cambrian trilobite faunas, including important and well-known taxa such as *Agraulos* Hawle & Corda, 1847, and *Paradoxides sensu lato*. *Sao hirsuta* Barrande, 1846, was earlier documented from the Czech Republic, Spain and Germany, and is now first described from western Avalonia, while *Bailiella aequalis* (Linnarsson, 1882) was already mentioned for eastern Newfoundland and is now illustrated for the first time. The specimens presented here were assigned to the orders Ptychopariida, Redlichiida and Corynexochida and include *Agraulos ceticephalus* (Barrande, 1846); *Jincella? applanata* (Hicks in Salter & Hicks, 1869); *Sao hirsuta* Barrande, 1846; *Bailiella aequalis* (Linnarsson, 1882); *Bailiella tenuicincta* (Linnarsson, 1879); *Meneviella venulosa* (Hicks, 1872); *Paradoxides davidis* Salter, 1863; *Plutonides hicksii* (Salter, 1866b); *Clarella venusta* (Billings, 1872); and *Acontheus inarmatus* Hutchinson, 1962.

KEY WORDS

Miaolingian,
Cambrian,
Canada,
Avalonia,
polymerid trilobites,
biostratigraphy,
new synonyms.

RÉSUMÉ

Biostratigraphie et taxonomie des trilobites polymères de la formation de Manuels River (Drumien, Cambrien moyen), Terre-Neuve, Canada.

La formation cambrienne moyenne de Manuels River est renommée pour sa faune de trilobites bien préservés. Nous présentons ici un assemblage nouvellement collecté de 1184 spécimens provenant de la localité type de Conception Bay South, Terre-Neuve, Canada. L'assemblage faunique comprend des informations détaillées sur les aires de répartition précises de chaque espèce. Ainsi, les zones de polymérides *Paradoxides davidis* et *Paradoxides hicksi* précédemment établies pour la région et les zones d'agnostides *Tomagnostus fissus*, *Hypagnostus parvifrons*, *Ptychagnostus atavus* et *Ptychagnostus punctuosus*, reconnues mondialement, sont maintenant précisément corrélées. La faune de polymères est comparable à celle d'autres régions d'Avalonia, de Baltica et partiellement du Gondwana. Notre analyse de l'assemblage faunique démontre qu'il est nécessaire de procéder à des révisions complètes des faunes de trilobites du Cambrien, y compris des taxons importants et bien connus comme *Agraulos* Hawle & Corda, 1847 et *Paradoxides sensu lato*. *Sao hirsuta* Barrande, 1846 a été précédemment documenté de la République Tchèque, de l'Espagne et de l'Allemagne, et est maintenant décrit pour la première fois de l'ouest d'Avalonia, tandis que *Bailiella aequalis* (Linnarsson, 1882) est déjà mentionné pour l'est de Terre-Neuve et est maintenant illustré pour la première fois. Les spécimens présentés ici ont été assignés aux ordres Ptychopariida, Redlichiida et Corynexochida et comprennent *Agraulos ceticephalus* (Barrande, 1846); *Jincella? applanata* (Hicks dans Hicks & Salter, 1869); *Sao hirsuta* Barrande, 1846; *Bailiella aequalis* (Linnarsson, 1882); *Bailiella tenuicinta* (Linnarsson, 1879); *Meneviella venulosa* (Hicks, 1872); *Paradoxides davidis* Salter, 1863; *Plutonides hicksii* (Salter, 1866b); *Clarella venusta* (Billings, 1872); et *Acontheus inarmatus* Hutchinson, 1962.

MOTS CLÉS

Miaolingien,
Cambrien,
Canada,
Avalonia,
trilobites polymères,
biostratigraphie,
synonymes nouveaux.

INTRODUCTION

In Newfoundland, eastern Canada, the Manuels River Formation of middle Cambrian (Drumian, Miaolingian) age is long known for its abundant, diverse and well-preserved trilobite assemblages (e.g., Howell 1925; Hutchinson 1962). Polymerids, such as *Paradoxides davidis* Salter, 1863, and *Plutonides hicksii* (Salter, 1866b), are still considered to be valuable index fossils for the biostratigraphy of the area, although agnostid trilobites are now used for global correlation (e.g., Geyer & Shergold 2000; Peng & Robinson 2000; Geyer & Landing 2001, 2004; Babcock *et al.* 2007; Geyer 2019).

The first bed-by-bed descriptions of the Manuels River Formation were executed by Howell (1925), based on trilobite assemblages at the type locality, at Conception Bay South (Fig. 1). While some of these specimens are still housed at the Smithsonian National Museum of Natural History, Washington DC, United States, the major part of Howell's material has not been located by Hildenbrand (2016) and is considered as lost.

Subsequent to Howell (1925), the sediment succession and faunal assemblage at the type locality of the Manuels River Formation have variously been documented (e.g., Hutchinson 1962; Martin & Dean 1988; Landing & Westrop 1998a; Hildenbrand 2012, 2016; Austermann 2016; Hildenbrand *et al.* 2021). The authors emphasized on the excellent preservation of trilobites, brachiopods, hyolithids, small shelly fossils and acritarchs, preserved in grey to black shale with minor interbedded calcareous concretions. While Martin & Dean (1988) focused on acritarchs, Bergström & Levi-Setti (1978) studied *Paradoxides davidis* Salter, 1863, and Hildenbrand

(2016) and Hildenbrand *et al.* (2021) revised agnostid trilobites. The specimens documented here were recently sampled bed-by-bed at the type locality by Austermann (2016) and Hildenbrand (2016).

GEOLOGICAL SETTING

The c. 10° north dipping Cambrian shallow- to deep-marine sediment succession exposed on the southeastern shore of Conception Bay, south-eastern Newfoundland, is majorly continuous (Hutchinson 1962; Anderson 1987) and non-conformably overlies Neoproterozoic rocks of the Holyrood Horst (Rose 1952; Hutchinson 1962; Nautiyal 1966; King 1988; Landing & Westrop 1998a).

Cambrian Strata exposed along the Manuels River valley are assigned to the Brigus, Chamberlain's Brook, Manuels River and Elliot Cove formations. The contact of the Manuels River Formation with the underlying Chamberlain's Brook Formation is unconformable (e.g., Landing 1996; Landing & Westrop 1998a, b; Landing *et al.* 2022), while that with the overlying "Elliot Cove Group" (Hutchinson 1962), or Elliot Cove formation (Hayes 1948; Austermann 2016), is either conformable (Hutchinson 1962) or unconformable (Landing & Westrop 1998b; Austermann 2016).

Hutchinson (1962) defined the Manuels River Formation (Howell's beds 36-125) as a combination of Howell's (1925) Long Pond (11.28 m thickness) and overlying Kelligrew Brook (9.45 m thickness) formations, with bed 26 [sic] as the base of the Manuels River Formation. We agree with Fletcher (1972b) and Martin & Dean (1988) that this must have been

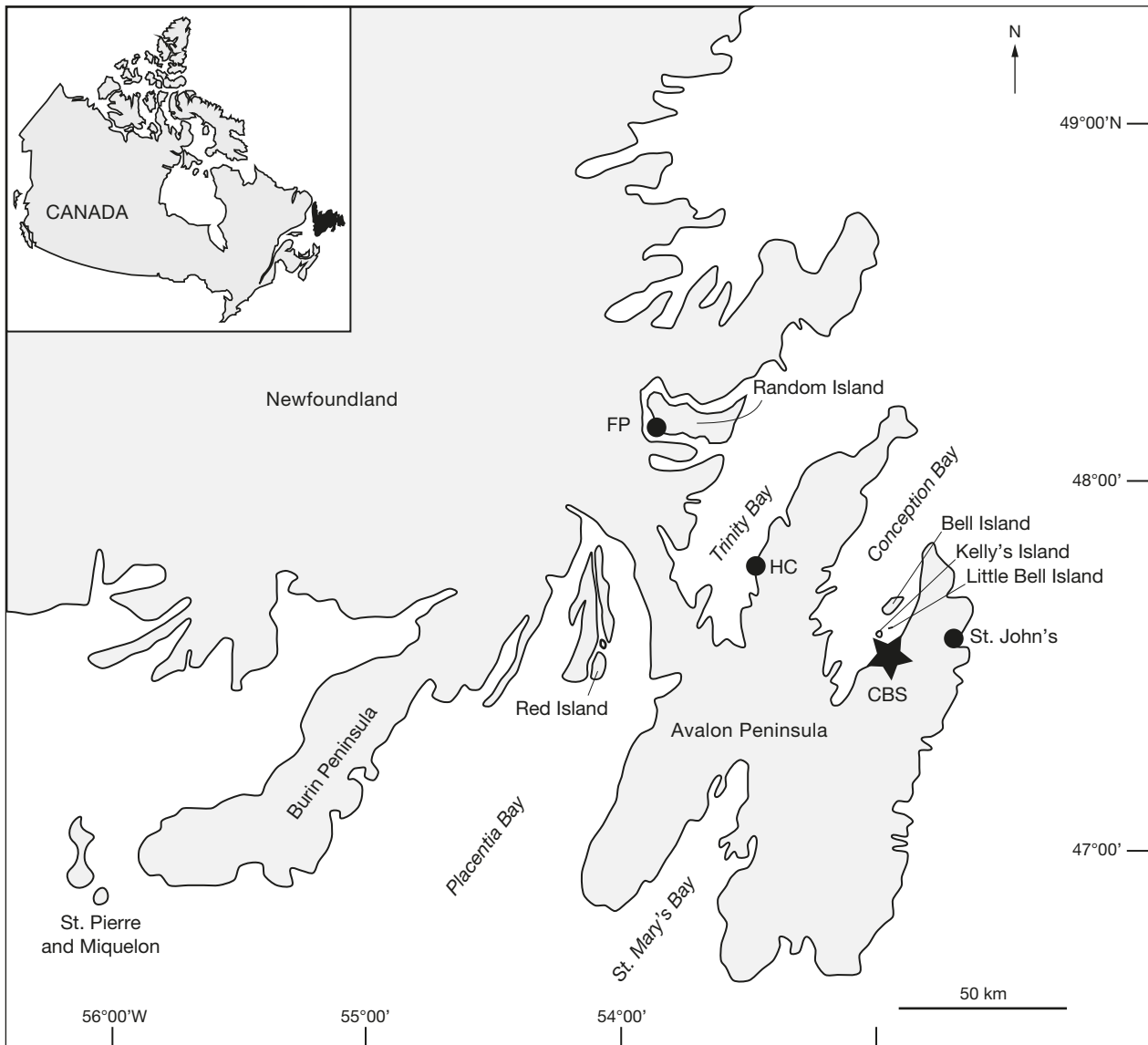


FIG. 1. — Map of Newfoundland with the Avalon and Burin peninsulas, the capital St. John's and the study area at Manuels River, Conception Bay South, Newfoundland, Canada (marked by a star). Abbreviations: **CBS**, Conception Bay South; **FP**, Fosters Point; **HC**, Highland Cove.

a typo. By Landing & Westrop (1998a) bed 125 is the remane sandstone that comprises the feather edge of the Cavendish Formation and is not part of the Manuels River Fm.

The Manuels River Formation is widely exposed in eastern Newfoundland, at e.g., Trinity Bay, the eastern part of Conception Bay, the western area of St. Mary's Bay, Placentia Bay, the southern part of Burin Peninsula, on Random Island, Red Island, Cape Breton Island (Nova Scotia), New Brunswick, and the islands of St. Pierre and Miquelon (Hutchinson 1962; Martin & Dean 1988; Fletcher 2006; Landing *et al.* 2022). In its type locality at Conception Bay South, the Manuels River Formation was measured to 19.07 m by Austermann (2016), but thickness may vary (e.g., 21.02 m by Landing & Westrop 1998a: fig. 7). For instance, 29–33 m thickness was presented for Fosters Point, Random Island, and Highland Cove, Trinity Bay (Hutchinson 1962). The lithology of the

Manuels River Formation (Fig. 2) has variously been presented as a sequence of highly fossiliferous grey to black mudstone, interbedded with calcareous concretions and volcanic ash deposits (Howell 1925; Hutchinson 1962; Fletcher 1972a, 2006; Austermann 2016).

The type locality of the Manuels River Formation is exposed in the valley of the Manuels River, located in the community of Manuels, Conception Bay South, Newfoundland, Canada at 47°31'30.7704"N, 52°57'4.5144"W (47.525214, –52.951254) (WGS 84). The base of the Manuels River Formation is there exposed c. 4 m above mean sea level (AMSL). The outcrop is approximately 20 m high and spans approximately 20 m along the river gorge. The valley, including the outcrop and its fossils, is under governmental protection by the Newfoundland and Labrador law, Regulation 67/11 "Palaeontological Resource Regulations under the Historic Resources Act".

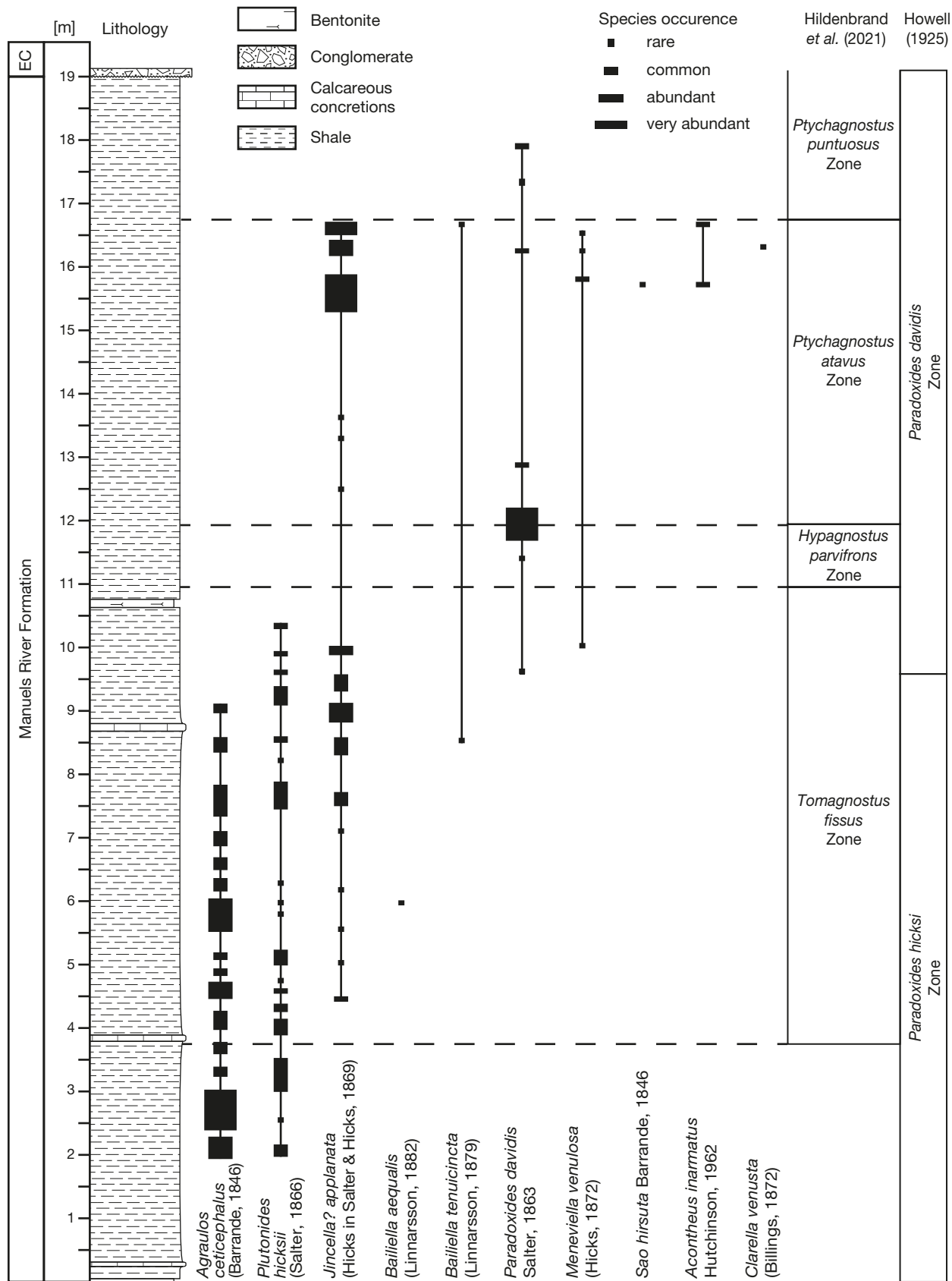


FIG. 2. — Lithology of the type locality of the Manuels River Formation, range chart of the here described species. Agnostid biozones from Hildenbrand *et al.* (2021) and polymerid biozones from Howell (1925).

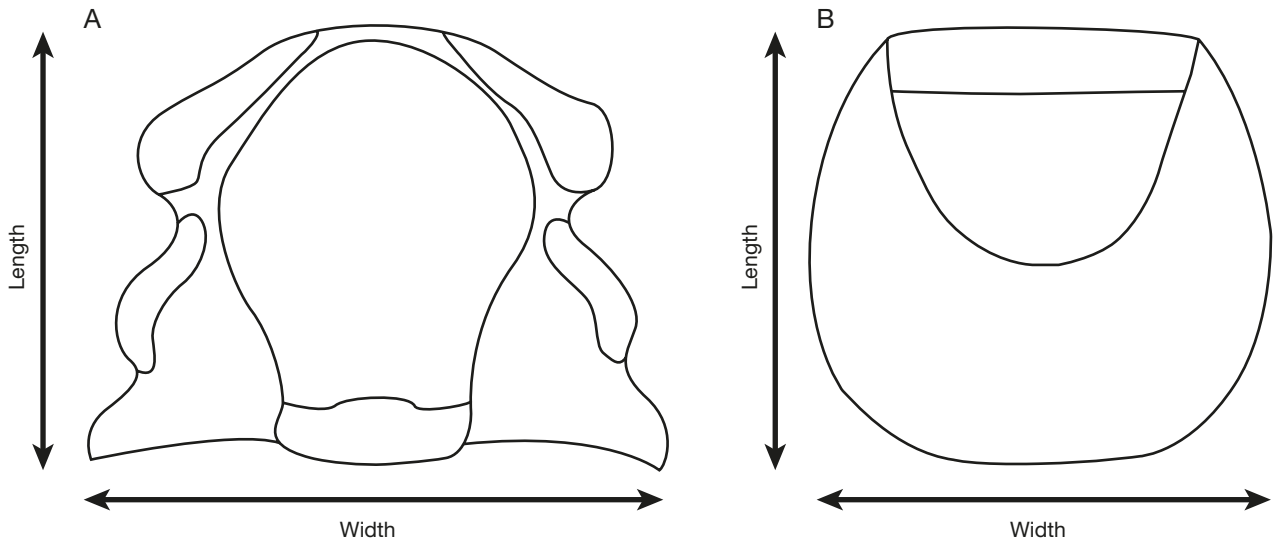


FIG. 3. — Visualization of measurement terms in cranidia (A) and pygidia (B).

MATERIAL AND METHODS

The fossil specimens described here (NFM F-2778–NFM F-3961, for further information see Appendix 1) were collected bed-by-bed by Austermann (2016) and Hildenbrand (2016) and are currently on loan to Heidelberg University as part of a formal agreement with The Rooms Corporation of Newfoundland and Labrador, Provincial Museum Division, Natural History Unit, St. John's, Newfoundland, Canada. The specimens were photographed with a camera or a KEYENCE digital microscope VHX-6000 using the fully automated depth of focus under direct light from the upper left. Adobe Photoshop CC 2020 was used for illustration of the photographs. The width of the specimens is measured at the widest point of the cephalon/cranidium, usually the anterior margin, and the widest point of the pygidium, respectively (Fig. 3). The length of the cephalon/cranidium is defined as the distance from the anterior frontal margin to the posterior end of the occipital ring (Fig. 3A). The pygidial length is measured from the first axial ring of the pygidium to the posterior margin (Fig. 3B).

INSTITUTIONAL ABBREVIATIONS

BGS	British Geological Survey, Keyworth, United Kingdom;
BGS(GSM)	British Geological Survey, Keyworth (old Geological Survey Museum collection, London), United Kingdom;
BM	British Museum, London, United Kingdom;
GSC	Geological Survey of Canada, Ottawa, Canada;
NFM	The Rooms Corporation of Newfoundland and Labrador, Provincial Museum Division, Natural History Unit, St. John's, Newfoundland, Canada;
NM L	National Museum, Prague, Czech Republic (previously SBNM);
SGU	Swedish Geological Survey (Sveriges Geologiska Undersökning), Uppsala, Sweden;
SM	Sedgwick Museum of Earth Sciences, Cambridge, United Kingdom.

SYSTEMATIC PALEONTOLOGY

Order PTYCHOPARIIDA Swinnerton, 1915

Suborder PTYCHOPARIINA Richter, 1933

Superfamily SOLENOPLEURACEA Angelin, 1854

Family AGRAULIDAE Howell, 1937

Genus *Agraulos* Hawle & Corda, 1847

Agraulos Hawle & Corda, 1847: 26, 27. — Type species: *Arion ceticephalus* Barrande, 1846, designated by Miller (1889).

Arion Barrande, 1846: 12, 13. — Type species: *Arion ceticephalus* Barrande, 1846, by monotypy (Barrande 1846).

Arionides – Barrande 1847: 391.

Herse Hawle & Corda, 1847: 19. — Type species: *Herse neubergii* Hawle & Corda, 1847, by monotypy (Hawle & Corda 1847).

Arionellus – Barrande 1852b: 404.

DIAGNOSIS. — Cranidium parabolic and domed; exoskeleton thick; glabella domed, equal-sided to trapezoidal; preglabellar field long; thorax of 16 segments (based on Lake 1932; Harrington *et al.* 1959; Fletcher 2017, with modifications).

REMARKS

The genus was first described by Barrande (1846) as *Arion*. As the name *Arion* was occupied by a genus of gastropods, Hawle & Corda (1847) renamed the trilobite *Arion* to *Agraulos*. Barrande (1847) corrected his mistake and renamed the genus to *Arionides*. Barrande (1852b) re-renamed the genus to *Arionellus*, as in his opinion *Arionides* might still be challenged by other authors. He rejected *Agraulos* Hawle & Corda (1847) as he found the name too similar to *Agraulis*, a genus of butterflies. Nevertheless, Pompeckj (1896) and Lake (1932) stated that a similarity of names, i.e. *Agraulos* and *Agraulis*, was not an adequate reason to reject the name given by Hawle & Corda (1947). Therefore, *Agraulos* is now the name established for this

genus. Lake (1932) mentioned that Hawle & Corda (1847) described juvenile forms of *Agraulos* as the new genus *Herse*.

The genus *Agraulos* is closely related to *Skreiaspis* Růžicka, 1946, but differs by a longer preglabellar field (Harrington *et al.* 1959). *Agraulos* is here included in the family Agraulidae Howell, 1937, following e.g., Harrington *et al.* (1959), Martin & Dean (1988), Jell & Adrain (2002), Bentley & Jago (2004) and Weidner & Nielsen (2014). The limiting of Agraulidae to a subfamily of the family Solenopleuridae Angelin, 1854, as proposed by Fletcher (2017), is not followed herein. This latter author suggested that the same characters that support Agraulidae, as defined by Bentley & Jago (2004), are also seen in *Parasolenopleura aculeata* (Angelin, 1851), the reference species of the Solenopleuridae. However, the Solenopleuridae has a deep occipital furrow and a narrow border (Harrington *et al.* 1959), which differ from a weakly to effaced occipital furrow and presence of a preglabellar field, as characteristically seen in the Agraulidae (Harrington *et al.* 1959; Bentley & Jago 2004).

Agraulos ceticephalus (Barrande, 1846)
(Figs 4; 5)

Arion ceticephalus Barrande, 1846: 12, 13; 1852b: 405–412.

Agraulos ceticephalus – Hawle & Corda 1847: 27; 1848: 143. — Miller 1889: 527. — Pompeckj 1896: 548, pl. 17, figs 12, 13. — Grönwall 1902: 158, 159, pl. 4, fig. 25. — Lorenz 1906: unnamed text fig. p. 67 upper right corner. — Walcott 1913: pl. 15, figs 1, 1a, b. — Wurm 1925: 87, 88, pl. 3, figs 16, 17. — Roch 1930: 132 (?). — Thorl 1935: 50, 51, pl. 3, fig. 12. — Prantl 1952: 262, 263, unnamed fig. p. 264. — Hupé 1953: fig. 120.1; 1955: fig. 96.2. — Šnajdr 1958: 174–177, fig. 37; pl. 36, figs 1–13; 1990: 106, unnamed fig. p. 107. — Horný & Bastl 1970: pl. 4, fig. 9. — Fletcher 1972b: pl. 69, figs 3, 4, 5a–c, 6, pl. 70, figs 1a, b, 2; 2006: pl. 34, fig. 35; 2017: 11–19, figs 5G–I, 6A–P, 7A–S, 8A–E, H–L, 16B, J, L (*partim*). — Whittington 1988: 594, text-fig. 14, pl. 55, figs 2, 4, 5, 8, 9; 1992: pls 7, 51. — Fatka 1990: unnamed fig. p. 13 upper right corner; 2011: fig. 17.6. — Müller 1994: 529, fig. 619. — Rudolph 1994: 217, pl. 24, fig. 5. — Cotton 2001: pl. 2, figs 4, 5. — Fletcher *et al.* 2005: 330, 331, figs 11.1–7. — Fatka *et al.* 2015: figs 4C, G.

Arionellus ceticephalus – Barrande 1852a: pl. 10, figs 6, 8–21; pl. 11, fig. 7 (*partim*). — de Verneuil & Barrande 1860: 526, 527, pl. 6, figs 13–17. — Gürich 1908: 19, pl. 5, fig. 2.

Arionellus longicephalus Hicks, 1872: 176, pl. 5, figs 20–26.

Agraulos longicephalus – Lake 1932: 157–159, pl. 20, figs 2, 7, 10. — Sdzuy 1961: 620–622, figs 32, 33. — Fletcher 1972b: pl. 68, figs 5a–d, 7–11; pl. 69, figs 1, 2; 2006: pl. 34, fig. 34; 2017: figs 22A, B. — Courtesole 1973: 138–140, pl. 10, figs 5, 6, 8–10; pl. 16, figs 12, 13. — Martin & Dean 1988: 21, 22, pl. 3, figs 10, 12, 13 (*partim*). — Rees *et al.* 2014: figs 1.8g, h. — Weidner & Nielsen 2014: 47, 48, figs 41A–F; 2015: 5–7, figs 3, 4A–L.

Agraulos longicephalus longicephalus – Liñan & Gozalo 1986: 78, pl. 35, figs 11–14; pl. 36, figs 4, 5 (*partim*).

Agraulos longicephalus brevilmbarus – Liñan & Gozalo 1986: 78, 79, pl. 35, figs 6–12; pl. 37, figs 1–8.

Agraulos (A.) ceticephalus – Schoenemann & Clarkson 2011: figs 5H, I.

Agraulos affinis – Fletcher 2017: fig. 11F.

Agraulos lewisi Fletcher, 2017: 19–21, figs 3A–C, 8F, G (*partim*), n. syn.

Agraulos socialis – Fletcher 2017: 23–27, figs 5J–L, 12A, K–Q, 13I–K, M, N, 14D, G, H, J, 16A, C.

Agraulos 1 – Fletcher 2017: figs 13D, E, 14A, 16F.

Agraulos 2 – Fletcher 2017: figs 14I, 15A–C, 16E (*partim*).

Skreiaspis punctatissimus – Fletcher 2017: figs 18S, U, W.

LECTOTYPE. — Specimen NM L 12581 (former ČC 345, No. 85 from SBNM collection Barrande), National Museum, Prague, Czech Republic, originally figured by Barrande (1852a) and designated as the lectotype by Šnajdr (1958). From the Buchava Formation, Skreje Member, *Eccaparadoxides pusillus* Zone from Skryje–Týřovice Basin, Bohemia, Czech Republic.

DIAGNOSIS. — Portion in front of cranium domed; front of glabella rounded to truncate; eyes distant at anterior half of glabella; pair of eye ridges expands from front of glabella towards eye lobes (based on Miller 1889; Fletcher 2017, with modifications).

MATERIAL EXAMINED. — 537 cranidia of *Agraulos ceticephalus* (for NFM numbers see Appendix 1). 24 specimens are attached to the thorax and seven have at least one librigena attached. The specimens are well to very well-preserved as internal casts and moulds. Some are pyritized and in a few the exoskeleton is preserved. All specimens range between 1.94 and 9.11 m (Fig. 2) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

OCCURRENCE. — *Agraulos ceticephalus* is a common middle Cambrian trilobite and has been documented from southeastern Canada, eastern Newfoundland, in the *Tomagnostus fissus* to *Ptychagnostus atavus* zones (Fletcher *et al.* 2005), *Ptychagnostus atavus* to *Hypagnostus parvifrons* zones (Fletcher 2017), and *Paradoxides hicksi* Zone (Fig. 2). It has also been reported from the United Kingdom in Wales (*Hypagnostus parvifrons* zone; Rees *et al.* 2014), Denmark (*Acidusus atavus* zone; Weidner & Nielsen 2014, 2015), in Bornholm (*Ptychagnostus punctuosus* zone; Rudolph 1994), France (Thorl 1935), Germany (Wurm 1925), the Czech Republic (*Eccaparadoxides pusillus* zone; e.g., Šnajdr 1990; Fletcher *et al.* 2005), and Spain (*Pardailhanian* and *Solenopleuropsis* zones; Liñan & Gozalo 1986).

DESCRIPTION

The cranidia range from 3.0 mm to 16.0 mm in width and from 2.0 mm to 11.0 mm in length. The shape of the glabella varies from slightly trapezoidal to more equal-sided, with a rounded to truncate front. Three to four pairs of glabellar furrows are preserved mainly in larger-sized specimens. In small-sized specimens, the glabella is steeply domed, while it is flatter in large-sized specimens. Nevertheless, the glabella is always more domed than the cheeks. Eye ridges, if preserved, initiate near the front of the glabella and connect with the eye lobes in a horizontal line, some line in a backwards angle towards the sides. The occipital ring points backwards roughly triangularly and the length of the spine varies with size. Some moulds of cephalon connected to the thorax spare spines to nodes on up to five axial segments. These and an ornamentation are usually preserved on moulds. Several cephalon show up to three variably pronounced grooves. One of these reaches from the front of the glabella to the anterior margin. The other two are developed towards the sides, varying in position. The front of the cranium is highly domed but a lateral view and microscope measurements indicate that this is an optical illusion and it is still rather flattened domed.

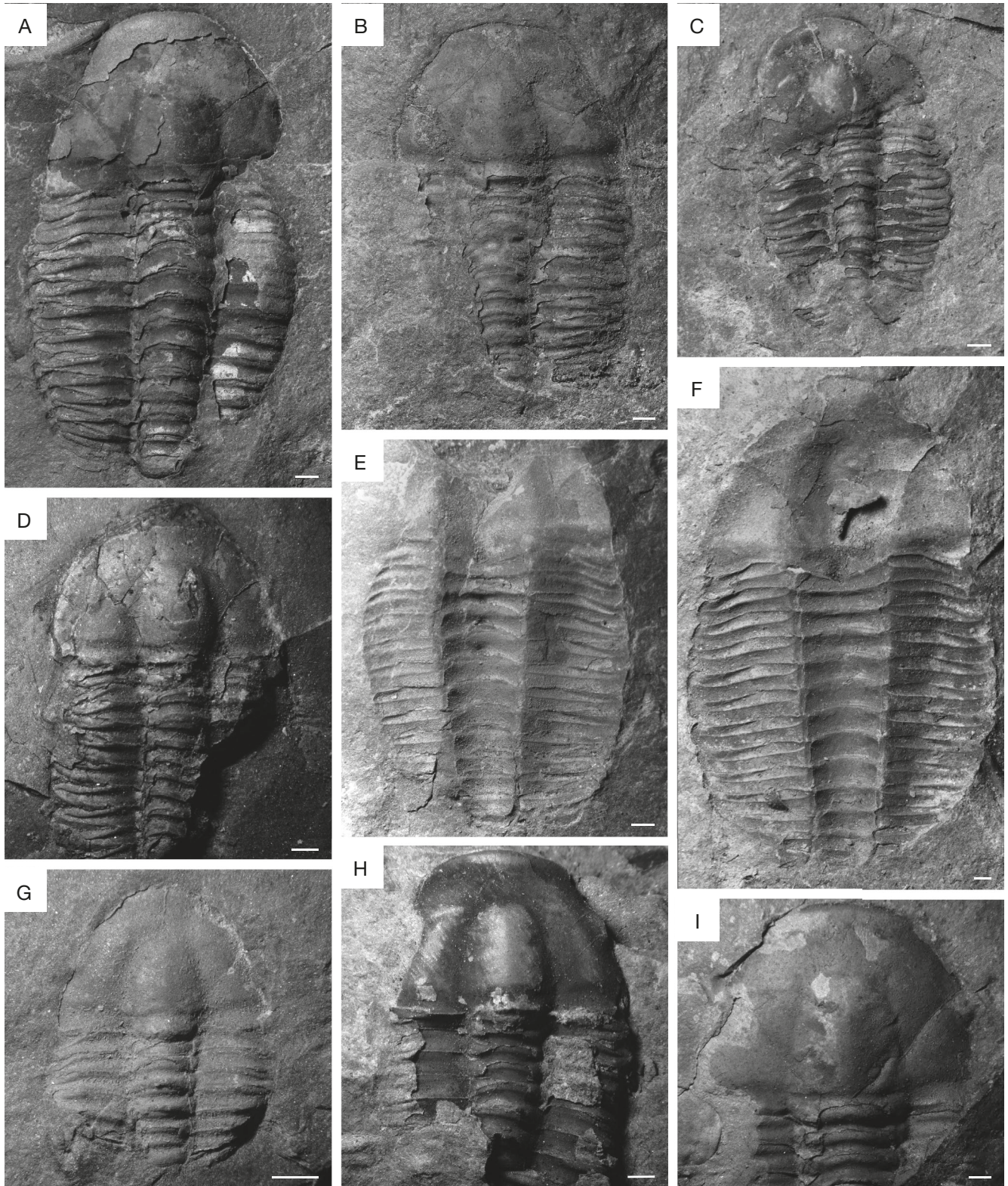


FIG. 4. — *Agrauius ceticephalus* (Barrande, 1846): **A**, internal cast of a cranidium attached to the thorax with preserved exoskeleton (NFM F-3476 from 5.97 m); **B**, internal cast of a cranidium attached to the thorax, partly covered with sediment, eye ridges and glabellar furrows slightly visible (NFM F-3951 from 7.10 m); **C**, internal cast of a cranidium attached to the thorax with preserved exoskeleton, eye ridges present (NFM F-3957 from 3.30 m); **D**, internal cast of a cephalon attached to the thorax, librigena attached, eye ridges present (NFM F-3621 from 9.08 m); **E**, mould of a cranidium attached to the thorax, spines on axial rings present, coarse ornamentation on thorax visible (NFM F-3476 from 5.98 m); **F**, mould of a cranidium attached to the thorax, occipital spine preserved (sedimentary filling laying in glabellar mould), coarse ornamentation on thorax visible (NFM F-3946 from 4.27 m); **G**, internal cast of a cranidium attached to the thorax, projection of axial spine preserved (NFM F-3831 from 7.43 m); **H**, internal cast of a cranidium attached to the thorax, eye ridges present (NFM F-2787 from 7.56 m); **I**, internal cast of a cranidium attached to first thoracic segments, eye ridges and glabellar furrows preserved (NFM F-3778 from 5.96 m). Scale bars: 1 mm.

REMARKS

Agraulos ceticephalus and *Agraulos longicephalus* are closely related species (e.g., Hicks 1872; Lake 1932; Sdzuy 1961; Weidner & Nielsen 2015) and both show a wide range of intraspecific variations, e.g. regarding the front of glabella or size and projection of the occipital spine (Barrande 1852b; Lake 1932; Sdzuy 1961). Barrande (1852b) documented ontogenetic changes in *Ag. ceticephalus*. He emphasized an increase in depth of the occipital furrow and dorsal furrows, less domed genal regions, and an increase in the thickness of exoskeletons in adult forms. The latter was also identified in *Ag. longicephalus* by Lake (1932). Accordingly, the development of glabellar, axial and other furrows as well as the occipital ring are not considered to be reliable diagnostic characteristics. Also, specimens with a preserved exoskeleton may show morphological details not identified in internal casts (Lake 1932; Sdzuy 1961). Despite the numerous descriptions and discussions about differences between *Ag. ceticephalus* and *Ag. longicephalus*, differentiation is hence questionable and this work agrees with Weidner & Nielsen (2014) that the genus *Agraulos* requires revision.

Barrande (1852a) illustrated several specimens of *Ag. ceticephalus*. The articulated specimens figured by the author on pl. 10, figs 1–5, and the cranidium on pl. 10, fig. 7, do not show the characteristic long preglabellar area of the genus *Agraulos* and are here excluded from *Ag. ceticephalus*, and even the genus. An enrolled specimen illustrated in lateral view of Barrande (1852a; pl. 10, fig. 21) shows no diagnostic characteristics and assignment to *Agraulos* is questionable. Hicks (1872) first described *Ag. longicephalus* based on a longer form and a more domed genal region than seen in *Ag. ceticephalus*. However, all cranidia figured by Hicks (1872), some attached to the thorax, are deformed, some elongated, and others compressed in length, as already mentioned by Fletcher (2017). The longer form of the cephalon is here interpreted as a result of tectonic deformation and the more domed genal region may also represent a preservational artefact. All seven type specimens illustrated by Hicks (1872) are here assigned to *Ag. ceticephalus*. Roch (1930) also referred to the similarity of *Ag. ceticephalus* and *Ag. longicephalus*. He compared specimens from Morocco and Algeria to *Ag. ceticephalus* from the type locality in Central Europe. Nevertheless, the assignment of the material to *Ag. ceticephalus* is questionable as no illustrations were presented by Roch (1930) and no information given regarding the number of studied specimens. Lake (1932) also discussed the morphological differentiation of *Ag. longicephalus* and *Ag. ceticephalus*. According to Lake (1932) *Ag. longicephalus* has an occipital ring ending in a triangular point and a more truncate glabella. However, Sdzuy (1961) suggested that the form of the occipital spine, or occipital node, is a variable characteristic and unsuited to define *Agraulos*. We here follow this latter view and interpret the more truncate glabella to fall within the intraspecific variation of *Ag. ceticephalus*. The presented specimens are here assigned to this latter species.

Sdzuy (1961) described a variable shape of the occipital ring of *Ag. longicephalus*, stating the shape as non-diagnostic. He followed Lake (1932) in that *Ag. longicephalus* is closely allied to *Ag. ceticephalus* but that the glabella of *Ag. longicephalus* is slightly

more narrowed towards the front, and mentioned a more domed genal region. We rather suggest that the domed genal region of *Ag. longicephalus* results from preservational bias and that the narrowed front of the glabella ranges within the intraspecific variation of *Ag. ceticephalus*. Hence, all cranidia illustrated by Sdzuy (1961) are here assigned to *Ag. ceticephalus*. Cranidia assigned to *Ag. longicephalus* by Fletcher (1972b) and Courtessole (1973) also show the characteristics of *Ag. ceticephalus* and are here assigned to this species. Liñan & Gozalo (1986) described two subspecies of *Ag. longicephalus* based on a more extended, respectively narrower preglabellar area compared to the border. These variations are also interpreted here as an intraspecific variation of *Ag. ceticephalus* and both subspecies are considered to be synonyms of the latter species. This interpretation includes cranidia, some attached to the thorax, illustrated by Liñan & Gozalo (1986: pl. 35, figs 11–14, pl. 36, fig. 4, pl. 36, fig. 5), whereas cranidia illustrated by the authors in plate 36, figs 1–3, do not show the long preglabellar field typical for *Agraulos* and are here excluded from the species and even the genus. Specimens documented by Martin & Dean (1988) as *Ag. longicephalus* are here assigned to *Ag. ceticephalus*, except for pl. 3, figs 9 and 11. These images display the same cranidium devoid of a wide preglabellar field and are therefore atypical for *Agraulos*. Fletcher (2006) displayed *Ag. ceticephalus* and *Ag. longicephalus*. The two cranidia figured by the author have distant eyes and a rounded to truncate glabella; the cranidium illustrated on pl. 34, fig. 34, is here assigned to *Ag. ceticephalus*. Specimens presented by Rees *et al.* (2014) and Weidner & Nielsen (2014, 2015) as *Ag. longicephalus* show the characteristics of *Ag. ceticephalus* and are hence assigned to this species.

Fletcher (2017) described and illustrated several species of *Agraulos*. The cranidium illustrated in fig. 11F was assigned to *Agraulos affinis* Billings, 1872, by Fletcher (2017), but the specimen has eyes distant to the glabella. This character disagrees with the diagnosis of *Ag. affinis*, in which eyes are located close to the glabella. Instead, the position of the eyes matches that seen in *Ag. ceticephalus* and the specimen is here assigned to this species. Specimens illustrated in fig. 9A–C as *Ag. ceticephalus*, on the other hand, display cranidia too deformed to determine the species. Specimens figured by Fletcher (2017: figs 9D–I) as *Agraulos lewisi* Fletcher, 2017 are also too poorly preserved to be assigned specifically. Figures 3A and 8F of Fletcher (2017) reillustrated the same articulate and distorted specimen figured previously by Lake (1932: pl. 20, fig. 3). Fletcher (2017) edited the images using Photoshop (Fletcher 2017: figs 3B, C, 8G). The figures 3C and 8G show the same image. The single specimen illustrated in figs 3A–C and 8F, G as *Ag. lewisi* clearly shows the characteristics of *Ag. ceticephalus*. The diagnosis of *Ag. lewisi* presented by Fletcher (2017) is not unique to the species, and characteristics as a “librigenal spine extending back to the posterior end of the third thoracic pleura” and “prominent stout median spines on the succeeding five rings” (Fletcher 2017) cannot be applied to the illustrations. Another characteristic, i.e. the “sharply pointed occipital spine”, is undiagnostic as discussed above. Consequently, *Ag. lewisi* is here interpreted to be a synonym of *Ag. ceticephalus*. Cranidia attributed by Fletcher (2017) to *Ag. longicephalus* and illustrated

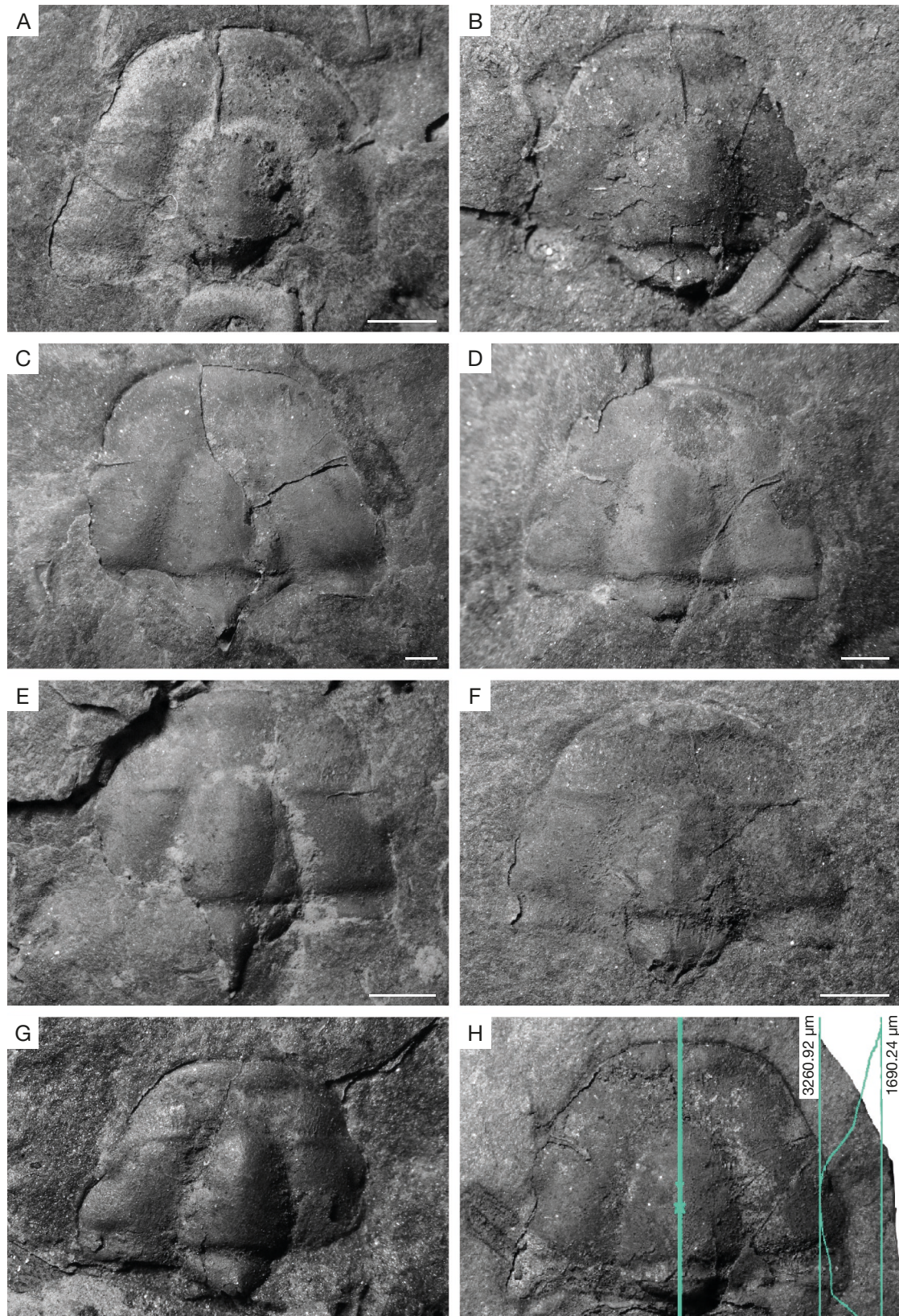


FIG. 5. — *Agrauios ceticephalus* (Barrande, 1846): **A**, internal cast of a cranidium, eye ridges present, two grooves visible (NFM F-2785 from 1.96 m); **B**, internal cast of a cranidium, one groove visible, occipital ring triangular in shape with projection of spine preserved (NFM F-3062 from 2.10 m); **C**, internal cast of a cranidium, occipital ring ending in a spine (NFM F-2841 from 2.40 m); **D**, internal cast of a cranidium, projection of occipital spine preserved (NFM F-2919 from 2.44 m); **E**, internal cast of a cranidium, eye ridges and occipital spine preserved (NFM F-2846 from 2.53 m); **F**, internal cast of a cranidium, eye ridges present, projection of occipital spine preserved (NFM F-3321 from 5.52 m); **G**, internal cast of a cranidium, eye ridges present, projection of occipital spine preserved (NFM F-2863 from 2.52 m); **H**, internal cast of a cranidium, two grooves visible, profile on the right shows that front is not as domed as it seems in overview (NFM F-3225 from 5.19 m). Scale bars: 1 mm.

in figs 22A, B show eye ridges characteristic of *Ag. ceticephalus* and are here assigned to this species. Fletcher's (2007: figs 5J-L, 12A, K-Q, 13I-K, M, N, 14D, G, H, J, 16A, C) display cranidia, or cranidia attached to the thorax, and were attributed by the author to *Agraulos socialis* Billings, 1872. Nevertheless, these illustrated specimens morphologically agree with *Ag. ceticephalus* and are here assigned to this species. A new species, *Agraulos 1* Fletcher, 2017, was introduced without a formal diagnosis or description. Fletcher (2017) only states that the "new species status is marked by the less trapezoidal aspect of the cranium with a longish occipital spine significantly different from associated similar-sized *ceticephalus* cranidia". These differences are here interpreted as intraspecific variations of *Ag. ceticephalus*. Therefore, the cranidia illustrated by Fletcher (2017: figs 13D, E, 14A, 16F) match the characteristics of *Ag. ceticephalus* and *Agraulos 1* is here interpreted as synonym of *Ag. ceticephalus*. Fletcher (2017) also described the new species *Agraulos 2* (Fletcher 2017: figs 14I, 15A-C, 16E) which is here also interpreted as an intraspecific variation of *Ag. ceticephalus*, while cranidia illustrated in figures 15D, E are too poorly preserved to be assigned to any species. Fletcher (2017) described *Skreiaspis punctatissimus* as a new species and illustrated several specimens. Cranidia illustrated in figures 18S, U and W do not show the short preglabellar field characteristic for *Skreiaspis*, but rather match *Ag. ceticephalus*.

Family SOLENOPLEURIDAE Angelin, 1854
Subfamily SOLENOPLEURINAE Angelin, 1854

Genus *Jincella* Šnajdr, 1957

Jincella Šnajdr, 1957: 241.

TYPE SPECIES. — *Solenopleura prantli* Růžička, 1946, by original designation.

DIAGNOSIS. — Glabella bluntly conical, not reaching frontal border; three pairs of shallow glabellar furrows; arched preglabellar area; arched cephalic border, widest in front of cranidium; ornamentation covering cranidium except for furrows and palpebral lobes; occipital ring with small node; thorax of 14 segments; pygidium small, with four to five rings on axis (based on Šnajdr 1957, 1958; Álvaro *et al.* 2004, with modifications).

REMARKS

The genus *Jincella* is closely related to the genus *Solenopleura* Angelin, 1854. *Jincella* has variously been treated as a junior synonym of *Solenopleura* (e.g., Rushton & Berg-Madsen 2002), while other authors (e.g., Geyer 1998; Álvaro *et al.* 2004) separated the two based on the relative convexity of the glabella, fixigenae, anterior border and eye lobes. Ornamentation is another reliable diagnostic characteristic in *Jincella*, even though this has been questioned by Fletcher (2007), who ranked *Jincella* as a subgenus to *Brunswickia* Howell, 1937. Based on the original description of Howell (1937) and images of the specimens assigned to the genus *Brunswickia*, the shape of the cranidium in *Brunswickia* is narrower than that of *Jincella*. We here follow Álvaro *et al.*

(2004) and interpret the presence of ornamentation of *Jincella* as a diagnostic characteristic. We therefore maintain the separation of *Jincella* from *Brunswickia* and *Solenopleura* and treat the genus as a member of Solenopleuridae, thus following e.g., Harrington *et al.* (1959), Courtessole (1973), Geyer (1998) and Álvaro *et al.* (2004).

Jincella? applanata (Hicks in Salter & Hicks, 1869)
(Fig. 6)

Conocoryphe applanata Hicks in Salter & Hicks, 1869: 53, 54, pl. 2, figs 1, 2, 4, 5.

Solenopleura applanata – Reed 1900: 252, 257. — Illing 1915: 432, pl. 37, figs 8, 9. — Nicholas 1915: 463, 464, pl. 39, figs 8, 9 (?). — Lake 1931: 137-139, pl. 17, figs 2-12. — Cobbold & Pocock 1934: 365, pl. 43, fig. 1 (?).

Solenopleura cf. applanata – Illing 1915: 433, pl. 37, fig. 10 (?).

Parasolenopleura? applanata – Martin & Dean 1988: 20, 21, pl. 1, fig. 14; pl. 3, figs 3, 6, 8, 14, 15.

Bailiaspis venusta – Cotton 2001: pl. 4, fig. 7.

Parasolenopleura applanata – Young *et al.* 2002: pl. 4, fig. x.

Parasolenopleura cf. applanata – Young *et al.* 2002: pl. 4, fig. iv.

Solenopleura cf. applanata – Rushton & Berg-Madsen 2002: 341, figs 5d-f.

Jincella applanata – Fletcher 2006: pl. 34, fig. 36.

Brunswickia (Jincella) applanata – Fletcher 2007: 50, 51, figs 7C-G, K-M, T.

Solenopleura? applanata – Weidner & Nielsen 2014: 82, 83, figs 50 A-I.

SYNTYPES. — Specimen BGS 7004 (British Geological Survey, Keyworth, United Kingdom) originally figured by Salter & Hicks (1869), counterpart BGS 7005 figured by Lake (1931) and SM A 271, A 3238 and A 3248 (Sedgwick Museum of Earth Sciences, Cambridge, United Kingdom). All syntypes were identified by Weidner & Nielsen (2014). From the Menevian of Port-y-rhaw, St. David's, Wales.

DIAGNOSIS. — Glabella parabolic, with three pairs of furrows; preglabellar field less wide than the associated anterior border; surface finely granulated with scattered granules (based on Salter & Hicks 1869; Fletcher 2007, with modifications).

MATERIAL EXAMINED. — 355 cranidia of *Jincella? applanata* (for NFM numbers see Appendix 1). Three are attached to the thorax and one has one librigena attached (NFM F-3595). The specimens are well to very well-preserved as internal casts and moulds. Some are pyritized. All specimens range between 4.44 and 16.67 m (Fig. 2) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

OCCURENCE. — *Jincella? applanata* is documented from south-eastern Canada, eastern Newfoundland, in the *Tomagnostus fissus*, *Ptychagnostus atavus*, *Paradoxides hicksi* and *Paradoxides davidis* zones (Martin & Dean 1988; Fletcher 2006, 2007). It has also been reported from the United Kingdom in Wales (Salter & Hicks 1869; Nicholas 1915; Young *et al.* 2002) and England (*Tomagnostus fissus* to *Solenopleura brachymetop* zones and *Ptychagnostus atavus* Zone; Illing 1915; Rushton & Berg-Madsen 2002), and from Denmark (*Acidusus atavus* Zone; Weidner & Nielsen 2014).

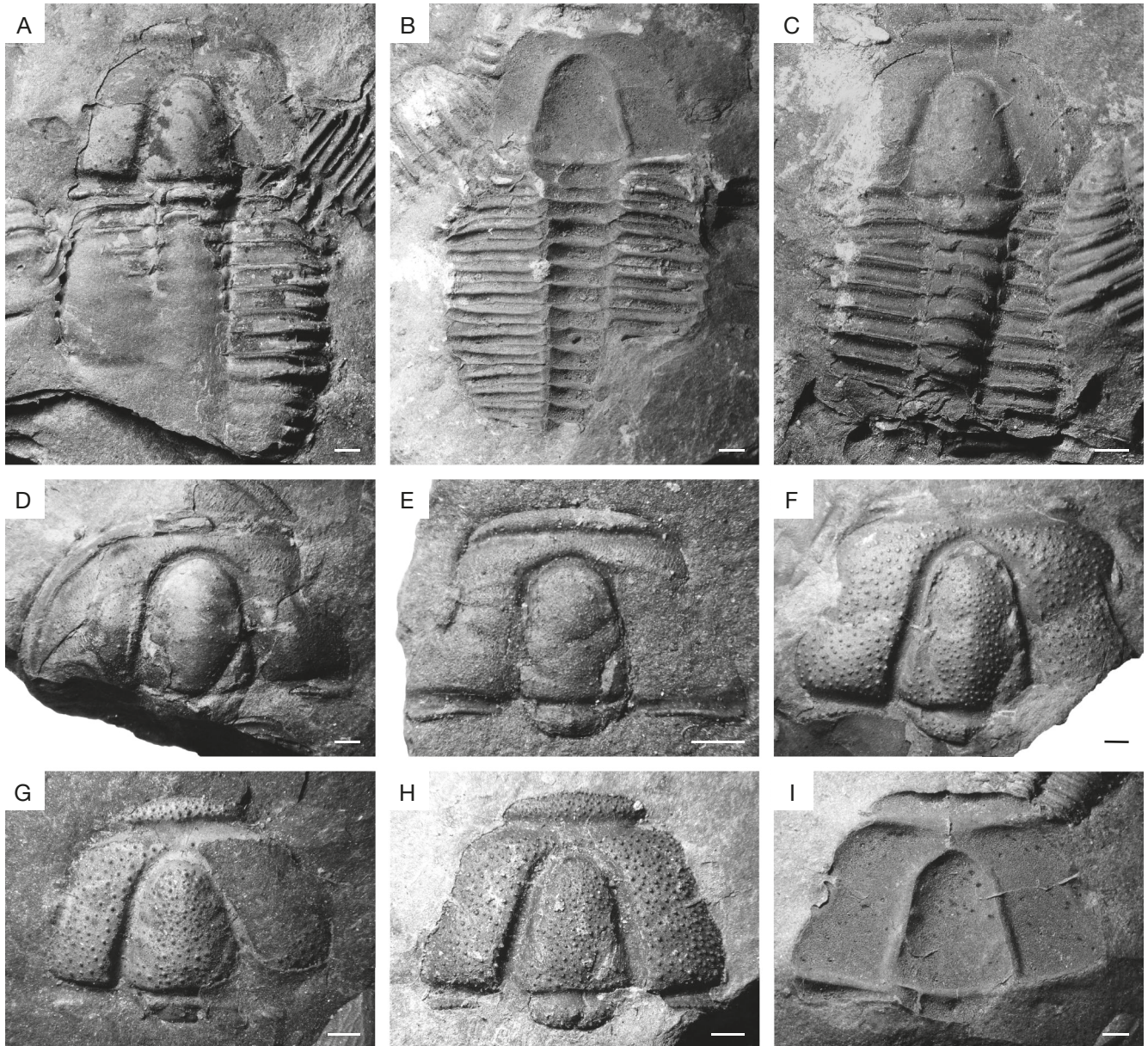


FIG. 6. — *Jincella? applanata* (Hicks in Salter & Hicks, 1869); **A, B**, internal cast and mould of the same specimen, glabellar furrows and ornamentation on internal cast preserved (NFM F-3398 from 8.94 m); **C**, internal cast of a cranidium attached to the thorax, ornamentation and occipital node preserved (NFM F-3401 from 8.94 m); **D**, internal cast of a cranidium with one librigena attached, venulose markings on librigena and cranidium anterior of eye ridges preserved (NFM F-3595 from 15.30 m); **E**, internal cast of a trapezoidal shaped cranidium, occipital ring and venulose markings anterior of eye ridges preserved, NFM F-3594 from 15.30 m; **F**, internal cast of trapezoidal shaped cranidium, densely packed scattered granules preserved, fixigenae slightly separated (NFM F-2949 from 6.15 m); **G**, internal cast of a round shaped cranidium, some granules have dents preserved, fixigenae slightly separated (NFM F-3297 from 6.18 m); **H**, internal cast of a round shaped cranidium, occipital ring and ornamentation preserved (NFM F-3616 from 9.33 m); **I**, mould of a round shaped cranidium, occipital node and ornamentation preserved (NFM F-3405 from 8.94 m). Scale bars: 1 mm.

DESCRIPTION

The size of the cranidium ranges from 3.5 mm to 16.0 mm width and from 2.1 mm to 12.0 mm length, while the cranidial shape varies from rounded to trapezoidal. In some rounded shaped cranidia the fixigena in front of the glabella are separated by a shallow depression from each other. Eye ridges are faint and frequently even absent in specimens with preserved ornamentation. Some moulds and occasional internal casts show vein-like markings in front of the eye ridges. One specimen (NFM F-3595) is preserved with an attached

librigena, also showing vein-like markings on the cranidium and the librigena. The glabella is always more domed than the cheeks. The posterior pair of glabellar furrows bend down slightly towards the occipital ring. The second pair of furrows only reaches half the length of the posterior ones and parallels these. The anterior pair is shortest and crosses the glabella more horizontally. Some specimens show a small node on the occipital ring. Where preserved, ornamentation consists of more or less densely packed scattered granules on the cephalon, and scattered granules on the thorax.

REMARKS

Jincella? applanata was first assigned to the genus *Conocoryphe* Hawle & Corda, 1847, by Salter & Hicks (1869). Reed (1900) discussed *Conocoryphe* and concluded that *J.? applanata* was better assigned to *Solenopleura* Angelin, 1854. Subsequent authors assigned the species to *Parasolenopleura* Westergård, 1953 (Martin & Dean 1988; Young *et al.* 2002), *Jincella* Šnajdr, 1957 (Álvaro *et al.* 2004; Fletcher 2006), or *Brunswickia* (*Jincella*) Šnajdr, 1957 (Fletcher 2007). Martin & Dean (1988) and Weidner & Nielsen (2014) marked the genus with a question mark, which reflects the uncertainty regarding the generic ranking. As pointed out by Rushton & Berg-Madsen (2002), Fletcher (2007) and Weidner & Nielsen (2014), among other authors, note that the family is in need for a revision. Therefore, the present material is here provisionally assigned to the genus *Jincella*. Regarding the authorship of the species, it is remarkable that several authors (e.g., Illing 1915; Lake 1931; Fletcher 2007) attribute it to Salter. In Salter & Hicks (1869), a H.H. abbreviation following the description of *J.? applanata* clarifies that Henry Hicks has written this part. Consequently, the correct authorship must be *J.? applanata* (Hicks in Salter & Hicks, 1869) as done by Weidner & Nielsen (2014).

Illing (1915) figured one juvenile cranidium assigned to *J.? applanata*. The image on pl. 37, fig. 10, is overexposed and the assignment therefore questionable. Nicholas (1915) presented drawings of two cranidia, both attached to the thorax. In his plate 39, figures 8, 9, the preglabellar area is relatively wide. This is unlike the diagnosis of *J.? applanata*, therefore the assignment is considered as questionable. Lake (1931) presented drawings of specimens previously figured by Salter & Hicks (1869), Nicholas (1915) and Illing (1915). These drawings show a preglabellar area wider than in the original figures. As Lakes' (1931) description matches *J.? applanata*, the wider preglabellar area is here considered to be a matter of uncertainty in the author's drawings. Cobbold & Pocock (1934) listed measurements of one illustrated specimen. The drawing of the cranidium has a wide preglabellar area and the eyes are situated close to the glabella. This does not match the characteristic short preglabellar area and the range of cranidial outlines known from *J.? applanata*. Therefore, the species-level assignment is questionable. Cotton (2001) figured one cranidium assigned to *Bailiaspis venusta* Resser, 1937, without presenting a description. However, the figured specimen has eyes and can therefore not be assigned to *Bailiaspis*, nor to its family Conocoryphidae Angelin, 1854. Instead, it matches *J.? applanata* and is here assigned to this species.

Subfamily SAOINAE Hupé, 1953

Genus *Sao* Barrande, 1846

Sao Barrande, 1846: 13. — Type species: *Sao hirsuta* Barrande, 1846, by original designation.

Monadina – Barrande 1846: 19.

Monadella – Barrande 1847: 391.

Crithias – Hawle & Corda 1847: 17.

Tetracnemis – Hawle & Corda 1847: 17.

Goniacanthus – Hawle & Corda 1847: 18.

Enneacnemis – Hawle & Corda, 1847: 19.

Acanthocnemis – Hawle & Corda 1847: 20.

Acanthogramma – Hawle & Corda 1847: 20.

Endogramma – Hawle & Corda 1847: 21.

Micropyge – Hawle & Corda 1847: 21.

Selenosema – Hawle & Corda 1847: 23.

Staurogmus – Hawle & Corda 1847: 28.

DIAGNOSIS. — Wide cephalic border, strongly convex; glabella with three deep glabellar furrows and one longitudinal furrow; preglabellar field concave without ornamentation; cephalon with densely packed tubercles and small spines; thorax of 17 segments; pygidium short with one segment and one terminal piece (based on Harrington *et al.* 1959; Laibl *et al.* 2014, with modifications).

REMARKS

Barrande (1852b) was the first to describe the different growth stages of *Sao*. He revised different genera previously introduced by Barrande (1846) and Hawle & Corda (1847). Šnajdr (1958) further described the wide morphological range of ontogenetic stages, which is followed here. For further details see Šnajdr (1958).

Richter (1941) made a formal request to the International Commission on Zoological Nomenclature in favour of *Sao* Barrande, 1846. He argued that the genus *Sao* Billberg, 1820, was preoccupied by a Stomatopoda, but that the name was not used subsequently. While *Monadina* Barrande, 1846 was available, *Sao* was already a well-established name for the trilobite. Richter's (1941) request was accepted and *Sao* Barrande, 1846 was given priority.

Sao hirsuta Barrande, 1846

(Fig. 7)

Sao hirsuta Barrande, 1846: 13. — Roemer 1876: pl. 1, figs 8a-e. — Woodward 1905: fig. 1. — Wurm 1928: 38, pl. 5, figs 11a, b; 1928: 38, figs 12a, b. — Whittington 1957: 937-940, pl. 115, figs 21, 22; pl. 116, figs 14-21; 1988: 591, 592, figs 13A-D; pl. 53, figs 5-7; 1992: pl. 35, figs A-I; pl. 36, figs A-D; pl. 37. — Šnajdr 1958: 205-214, figs 44.1-27, 45; pl. 42, figs 1-35; pl. 44, figs 1-25; pl. 45, figs 1-24 (see this work for further synonyms prior to 1958); 1990: 102, unnamed fig. p. 37; unnamed fig. upper right corner p. 45; unnamed fig. p. 103. — Harrington *et al.* 1959: figs 88A-I, 204.13a, b. — Horný & Bastl 1970: pl. 4, fig. 4. — Gil Cid 1982: 23, 24, figs 2a-e; pl. 1, figs 3-5. — Fatka 1990: unnamed fig. p. 16, unnamed fig. p. 17; 2011: figs 17.1-5, 7. — König 1992: pl. 1, fig. 3. — Gozalo *et al.* 1994: 48. — Sdzuy 2000: 310, pl. 5, figs 7-12. — Geyer 2010: 84, figs 12, 13. — Laibl 2012: 19-22, figs 6, 7; pl. 1, figs A-L; pl. 2, figs A-L; pl. 3, figs A-L; pl. 4, figs A-H; pl. 5, figs A-J; pl. 6, figs A-H; 2017: figs 4E-G. — Laibl *et al.* 2014: 297-302, figs 4A-L, 5A-L, 6A-F, 8A-F. — Fatka *et al.* 2015: fig. 4E.

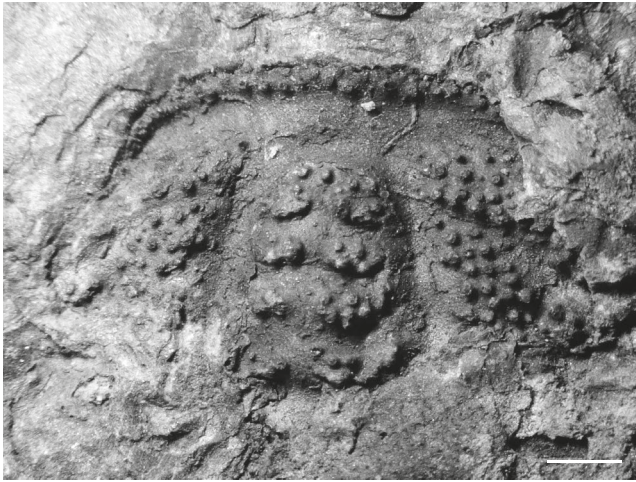


FIG. 7. — *Sao hirsuta* Barrande, 1846, internal cast of a cranidium (NFM F-3420 from 15.68 m). Scale bar: 1 mm.

Sao aff. *hirsuta* – Gozalo *et al.* 1994: 48-50, pl. 1, figs 2-6; pl. 2, figs 1-5.

LECTOTYPE. — Specimen NM L 12525 (former Br-184 from the SBNM collection Barrande), National Museum, Prague, Czech Republic, originally figured by Barrande (1852a) and designated as the lectotype by Šnajdr (1958). From the Buchava Formation, Skreyje Member, *Eccaparadoxides pusillus* Zone from Skryje- Týřovice Basin, Bohemia, Czech Republic

DIAGNOSIS. — As for the genus (Šnajdr 1958; Laibl *et al.* 2014).

MATERIAL EXAMINED. — One cranidium of *Sao hirsuta* (NFM F-3420). Collected at 15.68 m (Fig. 2) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

OCCURRENCE. — This is the first report of *Sao hirsuta* from eastern Newfoundland, Canada, where it is documented from the *Paradoxides davidis* Zone (Fig. 2). Elsewhere, the species is known from Europe where it was documented from the Czech Republic (*Eccaparadoxides pusillus* Zone; e.g., Šnajdr 1958), Spain (Gil Cid 1982; Gozalo *et al.* 1994), and Germany (Wurm 1928; Sdzuy 2000).

DESCRIPTION

The cranidium is 7.9 mm wide and 5.4 mm long. The glabella is 3.0 mm wide and 3.3 mm long. It is well-preserved as an internal cast and partly covered with sediment. The longitudinal glabellar furrow is not straight axially but slightly tending to the left posterior end of the glabella.

REMARKS

The ontogenetic development of the genus *Sao* and its species *Sao hirsuta* is well known (Warburg 1925). According to Šnajdr (1990), *S. hirsuta* has 22 synonyms which is one of the largest number of synonyms. For detailed list of synonyms, discussion and description of the species see Šnajdr (1958). This work follows his conclusions except for the works mentioned and added above. *Sao hirsuta* is common in the Czech Republic (e.g., Šnajdr 1958).

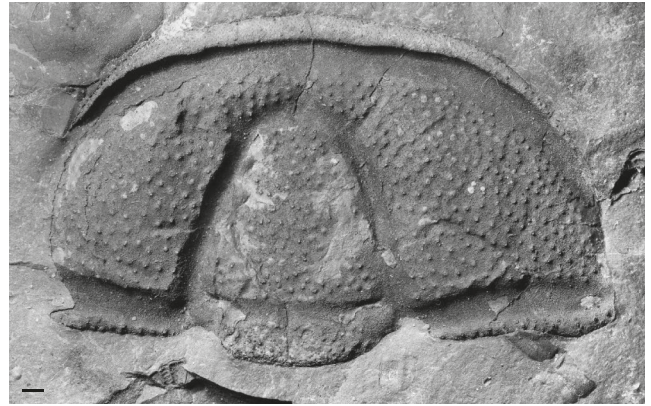


FIG. 8. — *Bailiella aequalis* (Linnarsson, 1882) internal cast of a cranidium (NFM F-3811 from 5.90 m). Scale bar: 1 mm.

Superfamily CONOCORYPHACEA Angelin, 1854 Family CONOCORYPHIDAE Angelin, 1854

Genus *Bailiella* Matthew, 1885

Bailiella Matthew, 1885: 124. — Type species: *Conocephalites baileyi* Hartt in Dawson, 1868, designated by Miller (1889).

Tangshiella Hupé, 1953: 194. — Type species: *Bailiella ulrichi* Resser & Endo, 1937, by original designation (Hupé 1953).

DIAGNOSIS. — Cephalon semicircular; fixed cheeks continuous in front of glabella; border furrow extends around cranidium; surface ornamented (based on Resser 1936; Lake 1940, with modifications).

REMARKS

Hupé (1953) introduced the genus *Tangshiella* without providing a description or discussion. The type species is *Bailiella ulrichi* Resser & Endo, 1937. The diagnosis of *B. ulrichi* matches that of the genus *Bailiella*; therefore, the genus *Tangshiella* is here considered to be a synonym of *Bailiella*. The genus is closely related to *Conocoryphe* Hawle & Corda, 1847, but differs in having a longer preglabellar area and the absence of furrows (Resser 1936). The taxonomic distinction from *Bailiaspis* Resser, 1936, is less distinct and presently unsolved (Resser 1936; Álvaro & Vizcaino 2018). Kim *et al.* (2002) regarded the genus *Bailiella* as paraphyletic and did not provide a diagnosis. Clearly, the genus requires revision. *Bailiella* is here treated as genus separated from related genera.

Bailiella aequalis (Linnarsson, 1882) (Fig. 8)

Conocoryphe aequalis Linnarsson, 1882: 25, 26, pl. 4, figs 12-15. — Grönwall 1902: 92, pl. 1, fig. 22.

Conocoryphe (C.) *aequalis* – Cobbold 1913: 32, pl. 3, figs 18a-c (?).

Bailiella aequalis – Westergård 1950: 28, 29, pl. 5, fig. 13; pl. 6, figs 1-3. — Rudolph 1994: 191, pl. 23, figs 6, 7 (?). — Sdzuy 2000: 308, pl. 3, figs 11-15; pl. 7, figs 4-6 (?).

Bailiella aff. *aequalis* – Šnajdr 1958: 166, pl. 35, figs 1-5.

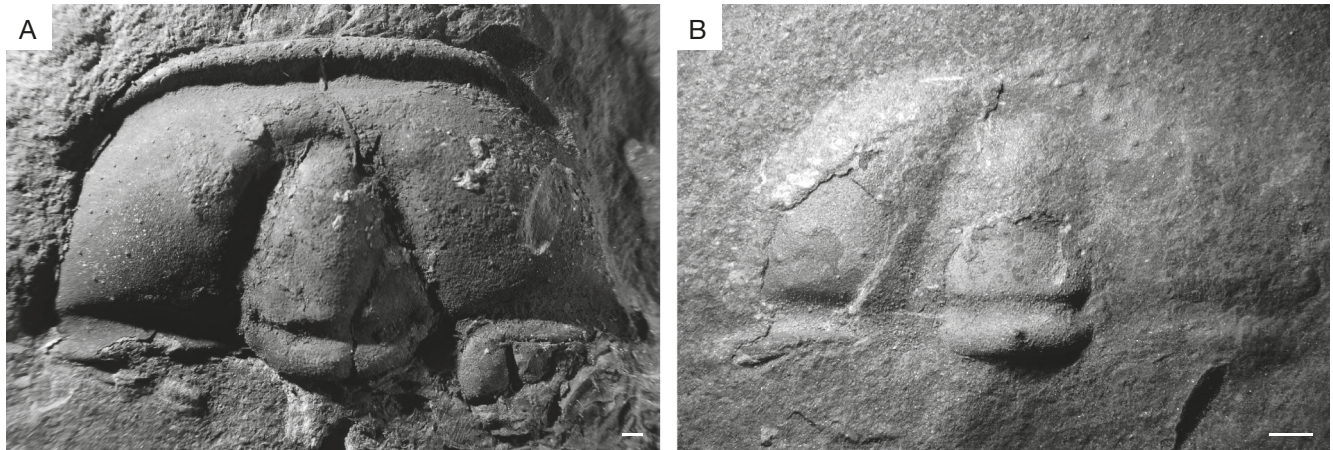


FIG. 9. — *Bailiella tenuicincta* (Linnarsson, 1879): **A**, internal cast of a cranium, scattered granules and occipital node preserved (NFM F-2972 from 8.52 m); **B**, internal cast of a cranium, scattered granules and occipital node preserved, partly covered with sediment (NFM F-3200 from 8.52 m). Scale bars: 1 mm.

LECTOTYPE. — Specimen originally figured by Linnarsson (1882: pl. 14, fig. 12) and designated as lectotype by Westergård (1950). From the *Ptychagnostus punctuosus* Zone, lower portion, Andrarum, Scania, Sweden.

DIAGNOSIS. — Cranium width/length ratio of *c.* 2/1; anterior margin narrow; occipital ring without node; packed coarse granulate ornamentation, grains with flattened to impressed top (based on Linnarsson 1882, with modifications).

MATERIAL EXAMINED. — One cranium of *Bailiella aequalis* (NFM F-3811). Collected at 5.90 m (Fig. 2) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

OCCURRENCE. — *Bailiella aequalis* is a rare middle Cambrian species (Westergård 1950), which is here documented from southeastern Canada, eastern Newfoundland, in the *Paradoxides hicksi* Zone (Fig. 2). It is also reported from United Kingdom, England (Cobbold 1913), Sweden (*Ptychagnostus punctuosus* Zone; Westergård 1950), Denmark in Bornholm (*Ptychagnostus punctuosus* Zone; Rudolph 1994) and Germany (Sdzuy 2000).

DESCRIPTION

The cranium is 40.0 mm wide and 21.0 mm long. The glabella is 11.0 mm wide and 12.0 mm long. It is very well-preserved as an internal cast, with an anterior margin that appears to be folded backwards.

REMARKS

Bailiella aequalis is closely related to *Bailiella tenuicincta* (Linnarsson, 1879), but differs by a shorter preglabellar area and packed granulate ornamentation. The ornamentation of *B. tenuicincta* is fine granulate with scattered grains (Linnarsson 1882). According to Linnarsson (1882) *B. aequalis* lacks a node on the occipital ring, differing from *B. tenuicincta* in which this node is present (Linnarsson 1879). Cobbold (1913) described *B. aequalis* based on six cranidia of which one was illustrated. He mentioned that these specimens were collected from a coarse sediment and that fine structures might therefore not be preserved. However, the shape of outline as well as the width/length ratio (*c.* 1.5/1) of the illustrated incomplete cranium on his plate 3, figure 18a, does not match *B. aequalis*. We therefore

regard the assignment as questionable. A pygidium illustrated by Rudolph (1994: pl. 23, fig. 7) as *B. aequalis* is doubtful as no diagnosis is known to us for the pygidium of this species. Sdzuy (2000) described and figured several cranidia of *B. aequalis*. As he also mentioned the fragment of a fixed cheek on plate 3, figure 15, cannot definitely be assigned to the species and hence the assignment is here considered questionable.

Bailiella tenuicincta (Linnarsson, 1879) (Fig. 9)

Conocoryphe tenuicincta Linnarsson, 1879: 18, 19, pl. 2, figs 23-25.

Bailiella tenuicincta – Westergård 1950: 26, 27, pl. 5, figs 6a-d, 7a, b, 8a, b, 9 (?). — Hutchinson 1962: 105, 106, pl. 15, figs. 3, 4a-d. — Rudolph 1990: 19, text-fig. 4; 1994: 192, 193, pl. 23, fig. 3 (?). — Weidner & Nielsen 2014: 74, fig. 43B.

Bailiella aff. *B. tenuicincta* – Martin & Dean 1988: 19, pl. 2, figs 7, 12.

Bailiella cf. *tenuicincta* – Chirivella Martorell *et al.* 2015: 177, figs 4A-I; p. 179, figs 5A, B.

LECTOTYPE. — Specimen no. SGU 4524, Swedish Geological Survey (Sveriges Geologiska Undersökning), Uppsala, Sweden, originally figured in Linnarsson (1879) and designated as lectotype by Westergård (1950). From the Exsulans Limestone Bed, *Tomagnostus gibbus* Zone, Gislöv, on the shore 1 km south of Brantevik, Scania, Sweden.

DIAGNOSIS. — Anterior margin narrow; glabella with three pairs of shallow to faint furrows; occipital ring with node; dense fine granulate ornamentation with scattered small granules (based on Linnarsson 1879, with modifications).

MATERIAL EXAMINED. — Four cranidia of *Bailiella tenuicincta* (NFM F-2972; NFM F-3168; NFM F-3169; NFM F-3200). All specimens range between 8.52 and 16.67 m (Fig. 2) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

OCCURRENCE. — *Bailiella tenuicincta* is a rare middle Cambrian taxon, documented from southeastern Canada, eastern Newfoundland, in the *Paradoxides hicksi* and *Paradoxides davidis* Zones

(Hutchinson 1962; Martin & Dean 1988). The taxon also occurs in Sweden (*Ptychagnostus* (*Triplagn.*) *gibbus* Zone; Westergård 1950, 1953), Bornholm in Denmark, (*Ptychagnostus* (*Triplagn.*) *gibbus* Zone; Westergård 1950; *Agnostus atavus* Zone; Weidner & Nielsen, 2014) and Spain (upper *Badulesia tenera* to lower *Badulesia granieri* zones; Chirivella Martorell *et al.* 2015).

DESCRIPTION

The cranidia range from 7.0 mm to 34.0 mm in width and 4.4 mm to 18.0 mm in length, while the glabella varies from 2.5 to 10.0 mm in width and 2.8 to 10.5 mm in length. All specimens are well to very well-preserved internal casts. One specimen (NFM F-2972) has two to three pairs of faint glabellar furrows. Posterior pair is aligned towards the occipital ring.

REMARKS

The species is closely related to *B. aequalis* as discussed above. According to Weidner & Nielsen (2014) the stratigraphic range of *B. tenuicincta* is similar to that of *Bailiella impressa* (Linnarsson, 1879), from which it differs in having an evenly convex cranidium and shallow axial and border furrows. Westergård (1950) figured three cranidia and one pygidium. Granulation of the pygidium (Westergård 1950: pl. 5, fig. 9) corresponds to that of the cranidia and is therefore assigned to the species, but this assignment is here considered questionable. A cranidium illustrated by Rudolph (1990: 19, text-fig. 4) may correspond to *B. tenuicincta*, but the resolution of the image is too low to evaluate the assignment and is therefore questionable.

Genus *Meneviella* Stubblefield, 1951

Meneviella Stubblefield, 1951: 213. — Type species: *Erinnys venulosa* Hicks, 1872, by monotypy.

Erinnys Hicks, 1872: 177. — Type species: *Erinnys venulosa* Hicks, 1872, by monotypy (Hicks 1872).

Salteria – Walcott 1884: 31.

Menevia – Lake 1938: 270–272.

DIAGNOSIS. — Body elongate; micropygous; cephalon semicircular, wide and convex; fixigena meet in front of glabella; eye ridges at anterior third of glabella, tapering away; pair of librigenal spines; thorax of 25 segments or more with narrowing axis; pygidium small, axis tapering (based on Harrington *et al.* 1959, with modifications).

REMARKS

Hicks (1872) first described *Erinnys venulosa*. The name *Erinnys* was occupied by Schrank & Schrank (1801) who named a genus of butterflies *Erynnis*. Walcott (1884) recognized the circumstances and renamed the genus *Salteria* in honour of Salter. However, *Salteria* was already in use for another trilobite described by Thomson (1864), which was mentioned by Lake (1938). Lake (1938) gave the name *Menevia* to the genus, but this name was preoccupied by Schaus (1928). Stubblefield (1951) introduced *Meneviella* as a new generic name, which is still recognized today.

Meneviella venulosa (Hicks, 1872)

(Fig. 10)

Erinnys venulosa Hicks, 1872: 177, pl. 6, figs 1–6. — Salter 1873: 5. — Illing 1915: 426.

Erinnys (*Harpides*) *venulosa* – Salter 1866a: 285 (?), *nomen nudum*.

Salteria venulosa – Walcott 1884: 31, 32.

Erinnys brevipes – Matthew 1899: 91–95, pl. 4, fig. 9.

Conocoryphe (*Erinnys*) *venulosa* – Grönwall 1902: 94–96, pl. 1, fig. 23.

Bailiella venulosa – Howell 1925: 30, 31 (?).

Menevia venulosa – Lake 1938: 272, pl. 39, figs 4–9; 1940: 273, 274. — Harrington *et al.* 1959: O244, fig. 181.10.

Menevia cf. *venulosa*; Kindle & Whittington 1959: fig. 3i (?).

Meneviella venulosa – Hutchinson 1962: 108, pl. 16, figs 2–7 (?). — Shaw 1966: 855, pl. 99, fig. 17. — Korobov 1973: 124–126, pl. 12, fig. 1. — Egorova *et al.* 1982: 110, pl. 3, fig. 10; pl. 9, fig. 10 (?). — Kindle 1982: pl. 1.2, fig. 7. — Morris & Fortey 1985: pl. 1, fig. 10. — Buchholz 1991: 222, pl. 2, fig. 2; 1997: 251, pl. 20, figs 7, 8. — Rudolph 1994: 197, 198, pl. 22, fig. 8 (?). — Cotton 2001: text-fig. 1A, pl. 3, figs 1–4. — Young *et al.* 2002: pl. 4, fig. xiii (?). — Fletcher 2006: pl. 34, fig. 37. — Weidner & Nielsen 2014: 75, 76, figs 44A–E. — Bushuev & Makarova 2016: 15, 16, pl. 1, fig. 4.

Meneviella viatrix Shergold, 1973: 21–25, pl. 10, fig. 1; pl. 11, figs 1–4; pl. 12, figs 1–8.

Dasometopus groenlandicus – Babcock 1994: 87, 88, fig. 7.3.

LECTOTYPE. — Specimen no. SM A1033, Sedgwick Museum of Earth Sciences, Cambridge, United Kingdom, originally figured in Hicks (1872) and designated as lectotype by Stubblefield (1951), from the Menevian of Port-y-rhaw, St. David's, Wales.

DIAGNOSIS. — Cranidium with wide border; glabella two thirds of cranidial length with three pairs of furrows, S1 curves back to occipital furrow axially, S2 and S3 short; occipital furrow arching forward axially; occipital ring with node; fixigena divided by ridges that run out from eye ridges, tapering backwards and spread out to anterior part by splitting into venulose markings, posterior part granulated.

MATERIAL EXAMINED. — 16 cranidia of *Meneviella venulosa* (for NFM numbers see Appendix 1). All specimens range between 10.00 and 16.55 m (Fig. 2) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

OCCURRENCE. — *Meneviella venulosa* has a wide middle Cambrian distribution and has been documented from southeastern Canada, eastern Newfoundland, in the upper *Paradoxides hicksi* to *Paradoxides davidis* zones (Hutchinson, 1962). It has also been reported from western Newfoundland (*Tomagnostus fissus* and *Ptychagnostus atavus* bearing Zone 3; Kindle 1982), United States of America in Vermont (*Paradoxides davidis* Zone; Shaw 1966), Greenland (*Ptychagnostus atavus* Zone; Babcock 1994), United Kingdom in Wales (*Hypagnostus parvifrons* to *Ptychagnostus punctuosus* zones; Thomas *et al.* 1984; Young *et al.* 2002) and England (*Paradoxides davidis* Zone; Illing 1915), Denmark in Bornholm (*Ptychagnostus punctuosus* Zone; Buchholz 1991; Grönwall 1902; Rudolph 1994), Russia in Siberia (*Tomagnostus fissus* to *Paradoxides hicksi* zones and *Anapolenus henrici* Zone; e.g., Egorova *et al.* 1982) and Australia in Queensland (*Ptychagnostus punctuosus* and *Goniagnostus nathorsti* zones; Shergold 1973).

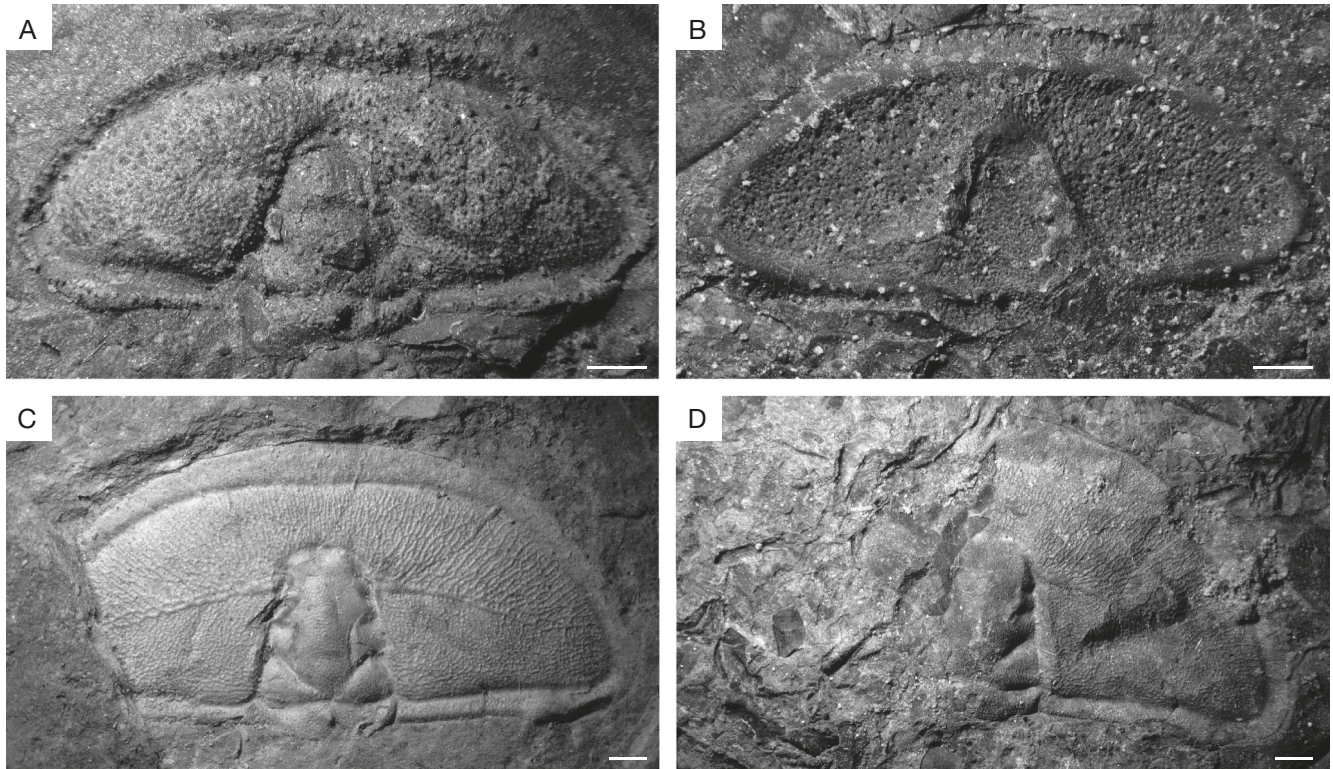


FIG. 10. — *Meneviella venulosa* (Hicks, 1872): **A, B**, internal cast and mould of the same juvenile specimen, venulose markings on mould visible (NFM F-3213 from 10.00 m); **C**, internal cast of cranidium, specimen covert in white (NFM F-3655 from 16.26 m); **D**, disarticulated internal cast of cranidium (NFM F-3600 from 15.73 m). Scale bars: 1 mm.

DESCRIPTION

The cranidia range from 11.0 mm to 17.0 mm width and from 4.5 mm to 8.0 mm length. They are well-preserved as internal casts and moulds. Some are broken along the dorsal furrow on one side of the glabella. In smaller specimens the venulose markings are less prominent and granulation covers the whole cranidium. Cranidia from stratigraphically lower beds (three cranidia from 10.00 m) have a more prominent granulation than those from stratigraphically higher beds (12 cranidia above 15.73 m). One internal cast has a white surface (NFM F-3655).

REMARKS

Salter (1866a) first reported *Erinnys* (*Harpides*) *venulosa* as a *nomen nudum*. He doubted that it could be distinguished from *Harpides* Beyrich, 1846, but without supporting this view by additional information, e.g. descriptions or figures. Thus, the assignment is questionable and Hicks (1872) is the author who first described the species. Matthew (1899) distinguished *Erinnys breviceps* from *Erinnys venulosa* based on the marginal furrow and border of the former, which, according to him, does not border the entire cranidium of *E. breviceps*. Matthew's plate 4, fig. 9 (Matthew 1899) illustrates a cranidium attached to the anterior portion of the thorax with a marginal furrow and border surrounding the whole cranidium. Therefore, the illustrated specimen is here assigned to *M. venulosa*. Howell (1925) reported specimens of Salter's *Erinnys venulosa* and named them *Bailiella venulosa* without providing a description

or illustrations. The assignment of his unfigured specimens is questionable. Kindle & Whittington (1959) illustrated one cranidium of *Menevia venulosa* which does not show the characteristic vein-like markings of the cephalon. Hence, the assignment is questionable. Note that Kindle & Whittington (1959) used *Menevia* in the figure description and *Meneviella* in the written text. Hutchinson (1962) described and illustrated different growth stages of *M. venulosa*, reporting that meraspid specimens (described as younger specimens by Hutchinson (1962)) show a more prominent granulation and less venulose markings than meraspid to holaspid specimens. The assumption that the specimen figured on Hutchinson's plate 16, figure 2 (Hutchinson 1962), is a young specimen of *M. venulosa* cannot be assigned with certainty due to the low resolution of the image.

Shergold (1973) described the new species *Meneviella viatrix*. According to the author, it differs from *M. venulosa* by a smaller size, fewer axial rings, more pygidial segments, and weaker geniculation in the posterior cranial margin. The body size is a questionable taxonomic characteristic (Müller 1994). In combination with the fewer axial rings, Shergold's (1973) almost completely articulated specimens may represent a late meraspid stage. Cephalons figured by Shergold (1973) are indistinguishable from *M. venulosa*, especially as no weaker geniculation (diagnostic character introduced by Shergold [1973]) is seen in the posterior cranial margin. The different number of axial rings may represent a different ontogenetic stage or represent a possible variation within

M. venulosa. Shergold (1973) only figured one disarticulated and two slightly deformed pygidia, all three attached to the thorax. The material is preserved and illustrated insufficiently to determine the number of pygidial axial rings. Therefore, *M. viatrix* is here interpreted to be a synonym of *M. venulosa*. One cranidium of *M. venulosa* figured by Egorova *et al.* (1982: pl. 3, fig. 10) is illustrated insufficiently. Therefore, the assignment is here considered questionable. Babcock (1994) defined the new species *Dasometopus groenlandicus*. The illustrated fragment in his figure 7.3 shows the vein-like markings of the cephalon characteristic for *M. venulosa* and was attributed to this species by Weidner & Nielsen (2014). Their suggestion is followed here. A small cranidium with a disarticulated glabella was illustrated as *M. venulosa* by Rudolph (1994: pl. 22, fig. 8), whose material includes several juvenile cranidia. The illustrated specimen does not show the characteristic vein-like markings of the cephalon. The case is similar to the incomplete cranidium illustrated by Young *et al.* (2002: pl. 4, fig. xiii). The illustrated specimen does not show the characteristic venulose markings, possibly due to the resolution of the illustration. In both cases, the assignment to *M. venulosa* is therefore questionable.

Order REDLICHIIA Richter, 1933

Suborder REDLICHIIA Richter, 1933

Superfamily PARADOXIDOIDEA Hawle & Corda, 1847

Family PARADOXIDIDAE Hawle & Corda, 1847

Genus *Paradoxides* Brongniart, 1822

Paradoxides Brongniart, 1822: 8. — Type species: *Entomostracites paradoxissimus* Wahlenberg, 1821, by subsequent designation by Poulsen (1956).

DIAGNOSIS. — Rounded anterior margin, S2 transglabellar, S3 and S4 short; palpebral lobe short, from S1 to S3; anterior and posterior section of facial suture moderately to strongly divergent; thorax with 19–21 segments; pleural spines progressively directed more strongly backwards, hindmost pairs of pleural spines increase in length, ending behind pygidial margin; pygidium small, subcircular to quadrat (based on Whittington *et al.* 1997; Fletcher *et al.* 2005, with modifications).

REMARKS

The genus *Paradoxides* Brongniart, 1822, and the family Paradoxididae Hawle & Corda, 1847, need comprehensive revision, as pointed out by e.g., Sdzuy (1967), Geyer (1998), Geyer & Landing (2001), Kim *et al.* (2002) and Żylińska & Masiak (2007). According to Żylińska & Masiak (2007), the main problem within *Paradoxides* are different characters for subdividing the species, such as subdivisions based on holaspid forms, in contrast to ontogenetic differences in protaspid and holaspid forms. Šnajdr (1958) mentioned a wide range in opinions (e.g., Pompeckj 1896; Raymond 1914) regarding the ontogenetic development of Czech *Paradoxides*. As discussed by Whittington *et al.* (1997), many specimens assigned to *Paradoxides* are too poorly preserved to be determined confidently, leading to several species being based on poorly

preserved material (Šnajdr 1958; Geyer 1998). According to Geyer & Landing (2001) there are more than 100 species and subspecies of *Paradoxides sensu lato*.

Šnajdr (1958) classified *Paradoxides* Brongniart, 1822; *Hydrocephalus* Barrande, 1846; *Eccaparadoxides* Šnajdr, 1957; and *Acadoparadoxides* Šnajdr, 1957, as genera of the Paradoxididae. Several authors followed this subdivision and included other genera as, for example, *Plutonides* Hicks, 1895 (e.g., Martinsson 1974; Whittington *et al.* 1997; Kim *et al.* 2002; Dean 2005; Rushton & Weidner 2007; Rushton *et al.* 2016). Others ranked clades as *Hydrocephalus*, *Eccaparadoxides*, *Acadoparadoxides*, and *Plutonides* as subgenera of *Paradoxides* (e.g., Solov'ev 1981; Martin & Dean 1988; Geyer 1998; Geyer & Landing 2001; Fletcher *et al.* 2005; Żylińska & Masiak 2007) and introduced new clades such as *Paradoxides* (*Mawddachites*) Fletcher, 2007 (Fletcher 2007). Kim *et al.* (2002) mentioned that diagnostic characteristics of (sub)genera differ substantially among authors. Here we apply the subdivision established by Whittington *et al.* (1997) following Šnajdr (1958).

Paradoxides davidis Salter, 1863

(Figs 11; 12)

Paradoxides davidis Salter, 1863: 276, unnamed text fig. p. 275; 1864a: 234, 235, pl. 12, figs 1–3; 1864b: 1–4, pl. 10, figs 1–8. — Linnarsson 1882: 11–14, pl. 1, figs 14, 15; pl. 2, figs 1–9. — Grönwall 1902: 106–112, pl. 2, figs 3–7. — Cobbold 1911: 287, pl. 24, figs 17a, b, 18. — Illing 1915: 428, pl. 35, figs 9–11 (?). — Lake 1935: 203–208, pl. 27, figs 1, 2; pl. 28, figs 1–3; pl. 29, figs 1–3. — Hutchinson 1952: 76, 77, pl. 2, figs 6–8; 1962: 115, pl. 19, fig. 10; pls. 20, 21; pl. 22, figs 1–5. — Hupé 1955: fig. 77.1. — Fletcher 1972b: 92, pl. 49, fig. 11; pl. 50, figs 1–6; pl. 51, figs 1, 2. — Bergström & Levi-Setti 1978: 6, 7.

Paradoxides davidis brevispinus Bergström & Levi-Setti, 1978: 11, fig. 7c; pl. 9, fig. 5; pl. 10, figs 1–7, **n. syn.**

Paradoxides davidis davidis Bergström & Levi-Setti, 1978: 7, 8, fig. 7a; pl. 2, figs 1–3; pl. 3, figs 1–5; pl. 4, figs 1–11; pl. 5, figs 1–11 (?). — Levi-Setti 2014: pls 150–154, **n. syn.**

Paradoxides davidis intermedius Bergström & Levi-Setti, 1978: 9, 11, pl. 6, figs 1–7. — Levi-Setti 2014: pl. 159, **n. syn.**

Paradoxides davidis trapezopyge Bergström & Levi-Setti, 1978: 8, 9, fig. 7b; pl. 6, fig. 8; pl. 7, figs 1–5; pl. 8, figs 1, 3, 4, 7, 8; pl. 9, figs 1–3. — Whittington 1992: 121, pl. 46. — Levi-Setti 2014: pls 155–158, **n. syn.**

Paradoxides (*Paradoxides*) *davidis davidis* – Morris & Fortey 1985: pl. 7, fig. 3, pl. 8, fig. 4 (?). — Martin & Dean 1988: 18, pl. 4, figs 11–17 (*partim*). — Fletcher 2007: 47, figs 8G–I. — Fletcher & Greene 2013: 514, pl. 3, figs 7, 9–11, 14, 15.

Plutonides hicksi – Vaněk *et al.* 1999: 36, pl. 1, figs 1, 2, 5, 6.

Paradoxides (*P.*) *davidis* – Fletcher 2006: 34, figs 9, 10. — Rees *et al.* 2014: figs 1.10, 1.11b.

HOLOTYPE. — Specimens no. BM 45083 and BM 45084, British Museum, London, United Kingdom by original designation, from the Menevian Group of Port-y-rhaw, St. David's, Wales, United Kingdom.

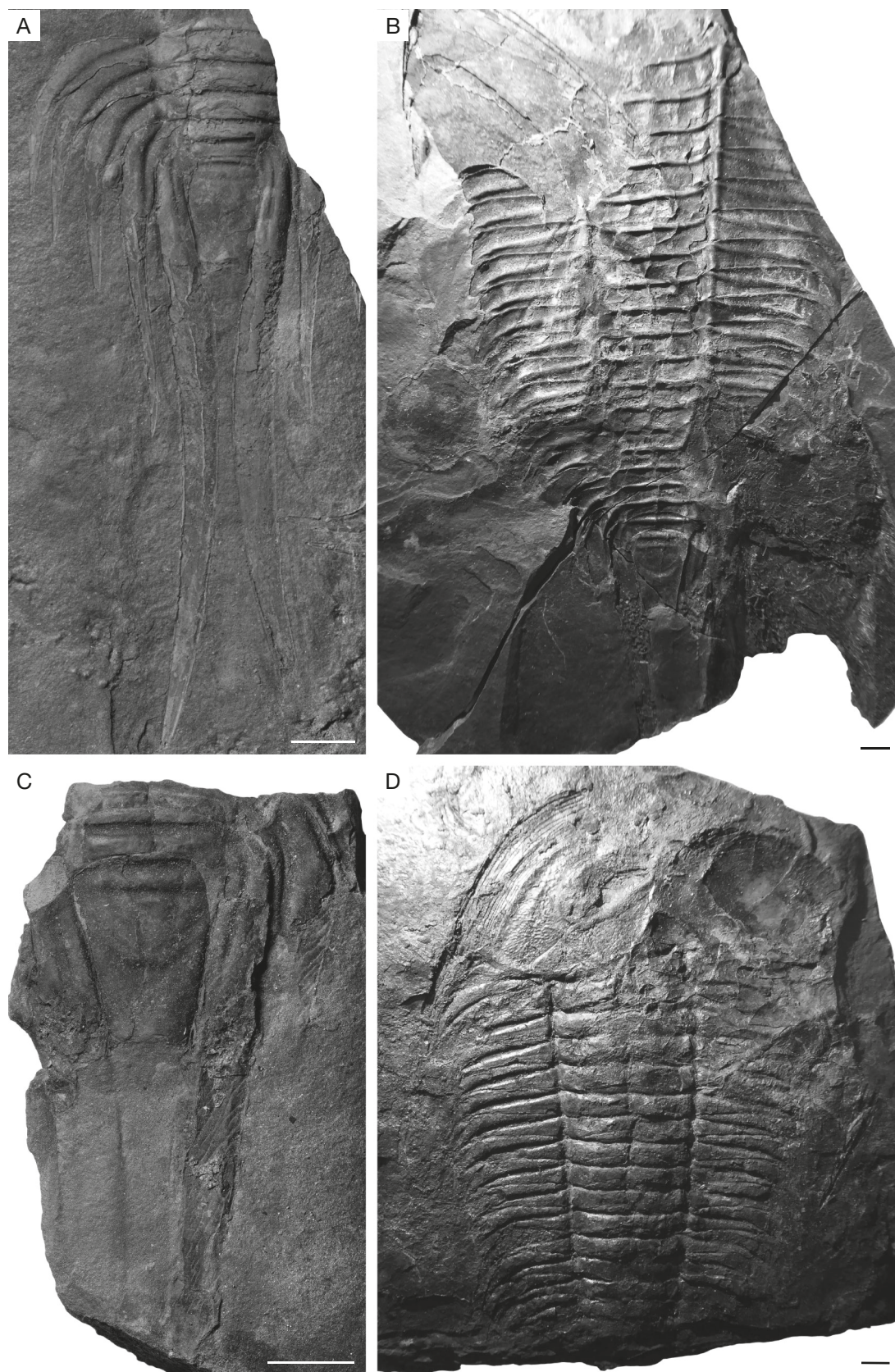


FIG. 11. — *Paradoxides davidis* Salter, 1863: **A**, internal cast of a pygidium attached to the posterior segments of the thorax (NFM F-3918 from 11.87 m); **B**, mould of a thorax with attached pygidium, thorax with preserved ornamentation (NFM F-3912 from 11.85 m); **C**, internal cast of a pygidium (NFM F-3909 from 15.05 m); **D**, internal cast of a thorax with dislocated cranium and librigenae, ornamentation on one librigena preserved (NFM F-2826 from 11.92 m). Scale bars: 5 mm.

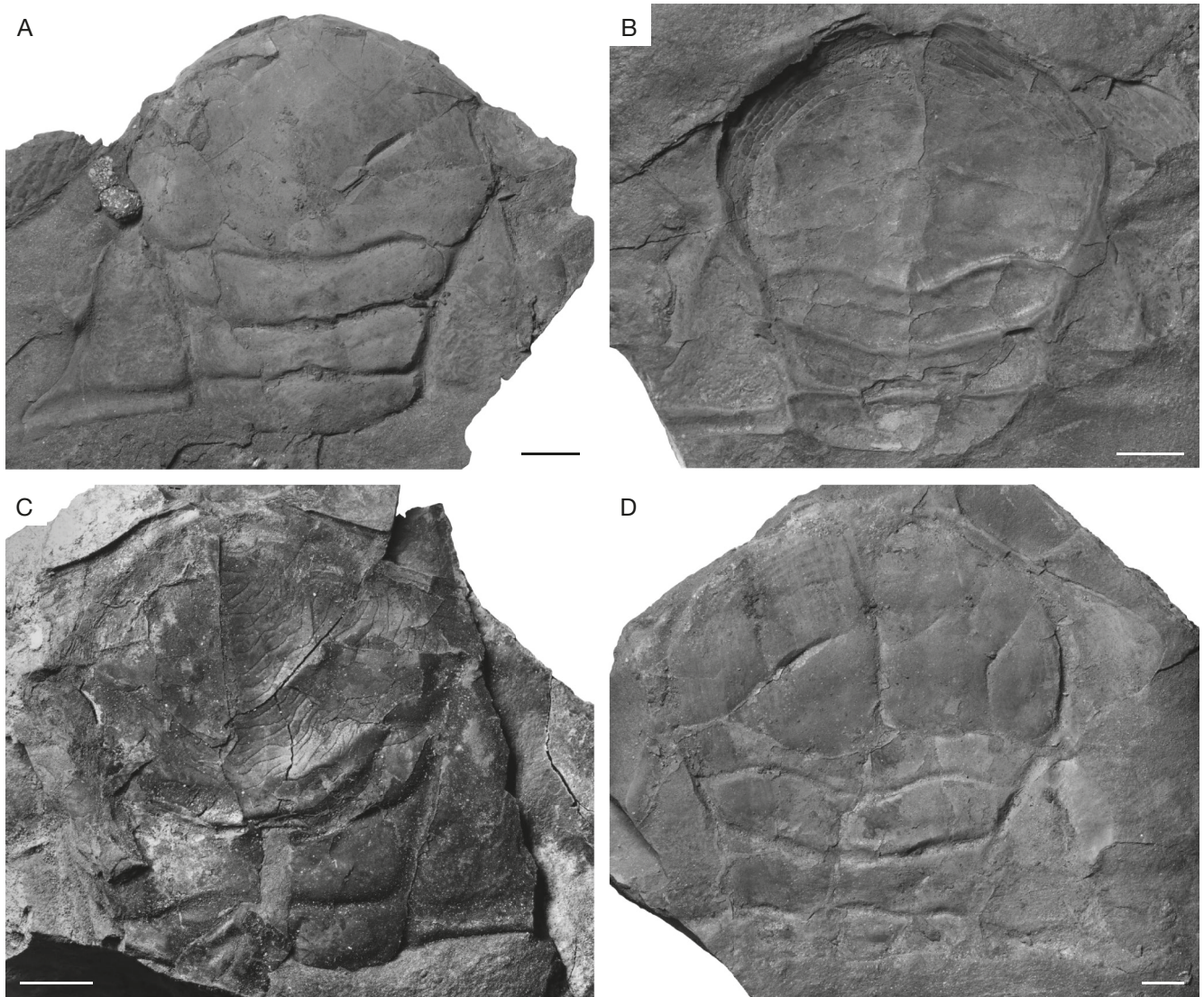


FIG. 12. — *Paradoxides davidis* Salter, 1863: **A**, internal cast of a cranidium, ornamentation on fixigenae preserved, occipital ring bears a node (NFM F-3842 from 11.19 m); **B**, mould of a cranidium, ornamentation on fixigenae and parts of doublure preserved (NFM F-3908 from 11.85 m); **C**, internal cast of a cranidium with doublure attached (NFM F-3663 from 12.06 m); **D**, internal cast of cranidium, occipital node slightly visible (NFM F-3934 from 12.08 m). Scale bars: 5 mm.

DIAGNOSIS. — Glabella with S1 curved backwards, S2 curved forward abaxially and backward axially, S3 and S4 absent; frontal lobe more than half of total glabellar length; occipital furrow curves slightly forward axially; librigenal spines and doublure lineated bifurcating and anastomosing, creating a narrow meshed net; thorax with 19 segments; posterior pleural spines extend far beyond pygidium; pygidium with concave posterior margin and axis with one ring (based on Lake 1935; Fletcher 1972b, with modifications).

MATERIAL EXAMINED. — 124 cephalons, mostly cranidia, some doublures, and seven pygidia of *Paradoxides davidis* (for NFM numbers see Appendix 1). All specimens range between 9.56 and 17.89 m (Fig. 2) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

OCCURRENCE. — *Paradoxides davidis* is an important regional biostratigraphical marker of the middle Cambrian (Howell 1925; Lake 1935; Hutchinson 1962), which has been documented from southeastern Canada, eastern Newfoundland, in the *Paradoxides davidis* and *Ptychagnostus punctuosus* zones (Hutchinson 1962; Fletcher 1972b; Martin & Dean 1988; Whittington 1992; Fletcher 2006,

2007; Fletcher & Greene 2013). It has also been reported from southeastern Canada in Nova Scotia (Hutchinson 1952), United Kingdom in Wales (*Paradoxides davidis* Zone; Salter 1863, 1864a; Lake 1935; Rees *et al.* 2014) and England (Cobbold 1911; Illing 1915), Denmark (Grönwall 1902), Sweden (*Ptychagnostus punctuosus* Zone; Linnarsson 1882; Westergård 1953) and the Czech Republic (*Eccaparadoxides pusillus* Zone; Vaněk *et al.* 1999).

DESCRIPTION

The cranidia range from 38.0 mm to 62.0 mm width and 31.0 mm to 55.0 mm length, while the pygidia range from 7.0 to 9.0 mm width and 10.0 mm to 12.0 mm length. The preservation of the cranidia is very good and the preservation of the pygidia is good, both preserved as internal casts and moulds. Some cranidial internal casts have a groove lining from the frontal margin across the glabella towards the middle to outer margin of the occipital ring. Some cranidia bear a small, macroscopically slightly visible node on the occipital ring. Several specimens are pyritized. The glabella is always

the most well-preserved part of the cranium. The pleural spines are usually broken. When preserved, the posterior pleural spines reach at least twice the pygidial length. Pygidia are shaped trapezoidally.

REMARKS

According to Lake (1935) *Paradoxides davidis* is closely related to *Paradoxides tessini* Brongniart, 1822. *Pa. tessini* has a longer palpebral lobe, a blunter front margin of the glabella, a less backward-curved S1 furrow, 21 thoracic segments and a rounded posterior margin of the pygidium (Lake 1935). Illing (1915) described and figured one doublure and two thoracic fragments of *Pa. davidis*. The fragment illustrated on pl. 35, fig. 10, only consists of four to possibly five outer pleurae without the axis, whereas the specimen on pl. 35, fig. 11, is overexposed. An assignment of the two specimens to any species is therefore questionable.

Bergström & Levi-Setti (1978) divided *Pa. davidis* into four subspecies: *Paradoxides davidis davidis*, *Paradoxides davidis trapezopyge*, *Paradoxides davidis intermedius* and *Paradoxides davidis brevispinus*. They distinguish them (*Pa. davidis davidis*, *Pa. davidis trapezopyge* and *Pa. davidis intermedius*) by their mean pygidial width ratio, while the fourth, *Paradoxides davidis brevispinus*, is distinguished by the mean pygidial width ratio, a coarse ornamentation and notably short pleural spines. We here propose, that the identification of this latter subspecies is thus only applicable when the pygidium is attached to the thorax and cephalon. The articulated specimens of *Pa. davidis davidis* figured by Bergström & Levi-Setti (1978: pl. 3, figs 1, 2) have poorly preserved cephalon and pygidia; their assignment to any species is here suggested questionable. Pygidial variations identified in *Pa. davidis*, as described by Bergström & Levi-Setti (1978), are herein interpreted as an intraspecific variation. The coarse ornamentation described by Bergström & Levi-Setti (1978) is not identified in all specimens assigned to *Pa. davidis brevispinus* (e.g., Bergström & Levi-Setti 1978: pl. 10, fig. 6), while it is visible on the thorax on their pl. 8, fig. 8, assigned to *Pa. davidis trapezopyge*. The presence, or absence of ornamentation is therefore here interpreted as either an intraspecific variation or a matter of preservation. The short pleural spines are not as notable as mentioned by Bergström & Levi-Setti (1978) and are consequently not considered to be a reliable diagnostic characteristic. Based on the here described 123 cranidia and only seven pygidia, none of them attached to the cephalon, we suggest that a division of *Pa. davidis* into subspecies is not applicable.

Pa. davidis davidis figured by Morris & Fortey (1985: pl. 7, fig. 3) is a poorly preserved mould of a cephalon attached to the anterior portion of the thorax, crossed by several cracks. The S2 furrow apparently is aligned parallel to the S1 furrow, which does not match the diagnosis of *Pa. davidis*. Based on the preservation and the shape of S2 the assignment to this species is questionable. Martin & Dean (1988) assigned their specimens to the subspecies *Pa. davidis davidis* but included all subspecies introduced by Bergström & Levi-Setti (1978) in their list of synonyms. The juvenile cranidium illustrated by Martin & Dean (1988) on plate 4, figure 4, has four gla-

bellar furrows and eye lobes reaching from S4 to L1. These characteristics do not agree with the diagnosis of *Pa. davidis* which is characterised by two characteristic glabellar furrows. The specimen is here excluded from the genus. The nearly articulated specimens documented by Whittington (1992) as *Pa. davidis trapezopyge* match the characteristics of *Pa. davidis* and are here assigned to the species. Vaněk *et al.* (1999) discussed and figured specimens assigned to *Plutonides hicksi* (Salter, 1866b). The illustrated cranidia on plate 1, figures 1, 2 and 6, only have S1 and S2 furrows with the typical shape of those of *Pa. davidis*; they are here assigned to *Pa. davidis*. Specimens illustrated by Fletcher (2007) and Fletcher & Greene (2013) assigned to *Paradoxides (Paradoxides) davidis davidis* show the characteristics of *Pa. davidis* and are hence assigned to this species.

Genus *Plutonides* Hicks, 1895

Plutonides Hicks, 1895: 230, 231. — Type species: *Plutonia sedgwickii* Hicks, 1871, designated by Whittington *et al.* (1997).

Plutonia Hicks, 1869: 69. — Type species: *Plutonia sedgwickii* Hicks, 1871, by monotypy.

Paradoxides (Mawddachites) Fletcher, 2007: 47. — Type species: *Paradoxides hicksii* Salter, 1866b, by original designation (Fletcher 2007).

DIAGNOSIS. — Surface ornamented; glabella widest at S4 furrow, frontal margin bluntly pointed; S2 to S4 present; palpebral lobes oblique, extending from S1 to S4; posterior section of facial suture sigmoidal; thorax with 19 segments; pygidium with one axial ring (based on Hicks 1869; Whittington *et al.* 1997, with modifications).

REMARKS

Plutonia was first described by Hicks (1869) but the name *Plutonia* was used by Stabile (1864) for a genus of Mollusca. Therefore, Hicks (1895) renamed the genus *Plutonides* which is still recognized today. Fletcher (2007) introduced the subgenus *Paradoxides (Mawddachites)* based on '*Paradoxides hicksii*' as type species. His diagnosis only includes *Pl. hicksii*. Diagnostic characteristics presented by the author included a glabella widest at S4, deep S1 to S4 furrows, palpebral lobes extending from the base of L5 to S1, a pygidium almost circular in outline and an exoskeleton ornamented with fine anastomosing venation or granulation. These characteristics match those given by Whittington *et al.* (1997) for *Plutonides*, e.g. the characteristic glabella widening to L4, well defined S2 to S4 furrows, palpebral lobes from L1 or S1 to S4, pygidium subhexagonal and a coarsely granulose surface with meshlike pattern of fine, anastomosing ridges. We therefore interpret *Paradoxides (Mawddachites)* as a synonym of *Plutonides*. The distinctly narrow occipital ring and the relatively narrow librigena extending backward into a long curving spine, as mentioned by Fletcher (2007) for *Pa. (Mawddachites)*, are here considered not to be diagnostic. Hicks (1869) already mentioned a close relationship between *Plutonides* and *Paradoxides*, but the author still referred to *Plutonides* as differing by its ornamentation of tubercles, unusual position of the eye suture and straight thoracic pleurae. Fletcher *et al.* (2005)

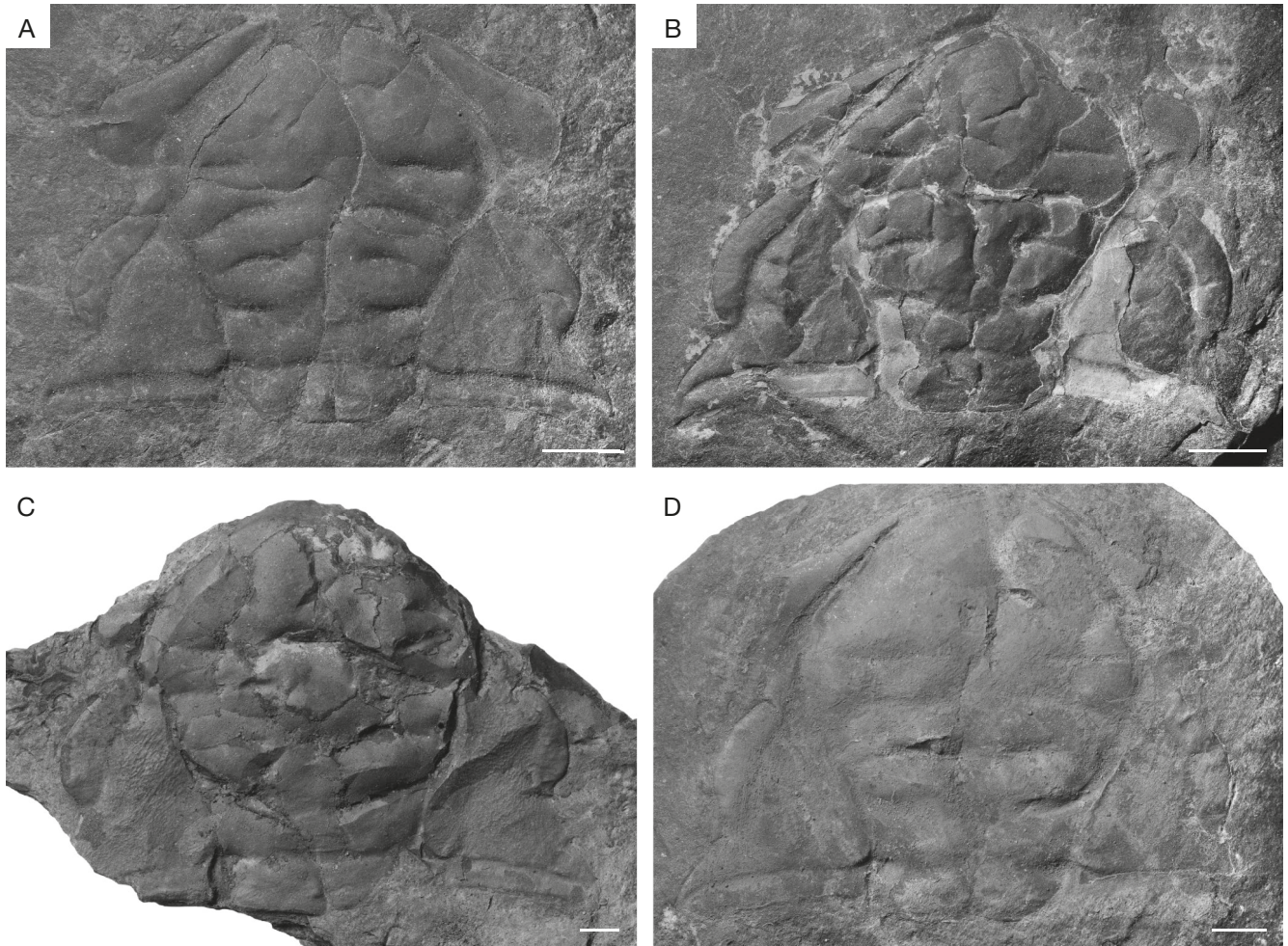


FIG. 13. — *Plutonides hicksii* (Salter, 1866b); **A, B**, internal cast and mould of the same specimen, occipital node visible in both (NFM F-3717 from 10.38 m); **C**, internal cast of a thorax attached to the pygidium, pleural spines preserved, NFM F-3299 from 5.22 m; **D**, internal cast of a cranidium attached to the anterior 11 thoracic segments (NFM F-3352 from 7.56 m). Scale bars: 5 mm.

ranked *Plutonides* as subgenus of *Paradoxides*, but this view is not followed here. *Plutonides* does not have a transglabellar S2 furrow, which is characteristic for *Paradoxides*. Other diagnostic differences in *Plutonides* are a shorter palpebral lobe and a bluntly pointed frontal margin compared to a rounded in *Paradoxides*. They clearly mark the separation of the genus *Plutonides* from *Paradoxides*.

***Plutonides hicksii* (Salter, 1866b)**
(Figs 13; 14; 15)

Paradoxides hicksii Salter, 1866b: 299, 300, pl. 4, fig. 12. — Salter & Hicks 1869: 55, pl. 3, figs 1-10. — Linnarsson 1882: 14, 15, pl. 3, figs 1-5. — Grönwall 1902: 117, 118. — Illing 1915: 428, 429, pl. 36, figs 1-7. — Nicholas 1915: 467, 469.

Paradoxides hicksii var. *palpebrosus* — Linnarsson 1879: 9-11, pl. 1, figs 5-11.

Paradoxides hicksi — Cobbald 1913: 47, 48, pl. 4, figs 1-5. — Lake 1934: 196, pl. 25, figs 4-9 (?); 1935: 197-200, pl. 36, figs 1, 2, 2a. — Hutchinson 1952: 76, pl. 2, fig. 5(?); 1962: 113, 114, pl. 18,

figs 4-12; pl. 19, figs 1, 2. — Egorova *et al.* 1982: 77, pl. 1, figs 4-6; pl. 2, figs 10, 11; pl. 3, figs 11, 12.

Hydrocephalus hicksii — Fletcher 1972b: 93, 94, pl. 47, fig. 15; pl. 48, figs 2-6; pl. 49, figs 1-5, 7-10 (?).

Paradoxides (*Paradoxides*) *hicksii* — Morris & Fortey 1985: 7, fig. 2.

Paradoxides (*Hydrocephalus*) *hicksii* — Martin & Dean 1988: 19, pl. 3, figs 4, 7.

Plutonides hicksii — Whittington *et al.* 1997: figs 306.1a-c. — Young *et al.* 2002: pl. 4, figs xi, xii. — Rushton *et al.* 2007: fig. 8e (*non* Vaněk *et al.* 1999: 36, pl. 1, figs 1-6).

Paradoxides (= *Plutonides*) *hicksii* (sic) — Bridge *et al.* 1998: pl. 8, figs g-h, j.

Paradoxides (subgen. nov.) *hicksii* (sic) — Fletcher 2006: pl. 34, figs 6-8.

Paradoxides (*Mawddachites*) *hicksii* — Fletcher 2007: 48, figs 8A-F. — Rees *et al.* 2014: figs 1.5g, h, j.

Mawddachites hicksii — Weidner & Nielsen 2014: 80, 81, fig. 48.

Paradoxides aff. *hicksi* — Bushuev & Makarova 2016: 20, 21, pl. 1, figs 7, 7a.

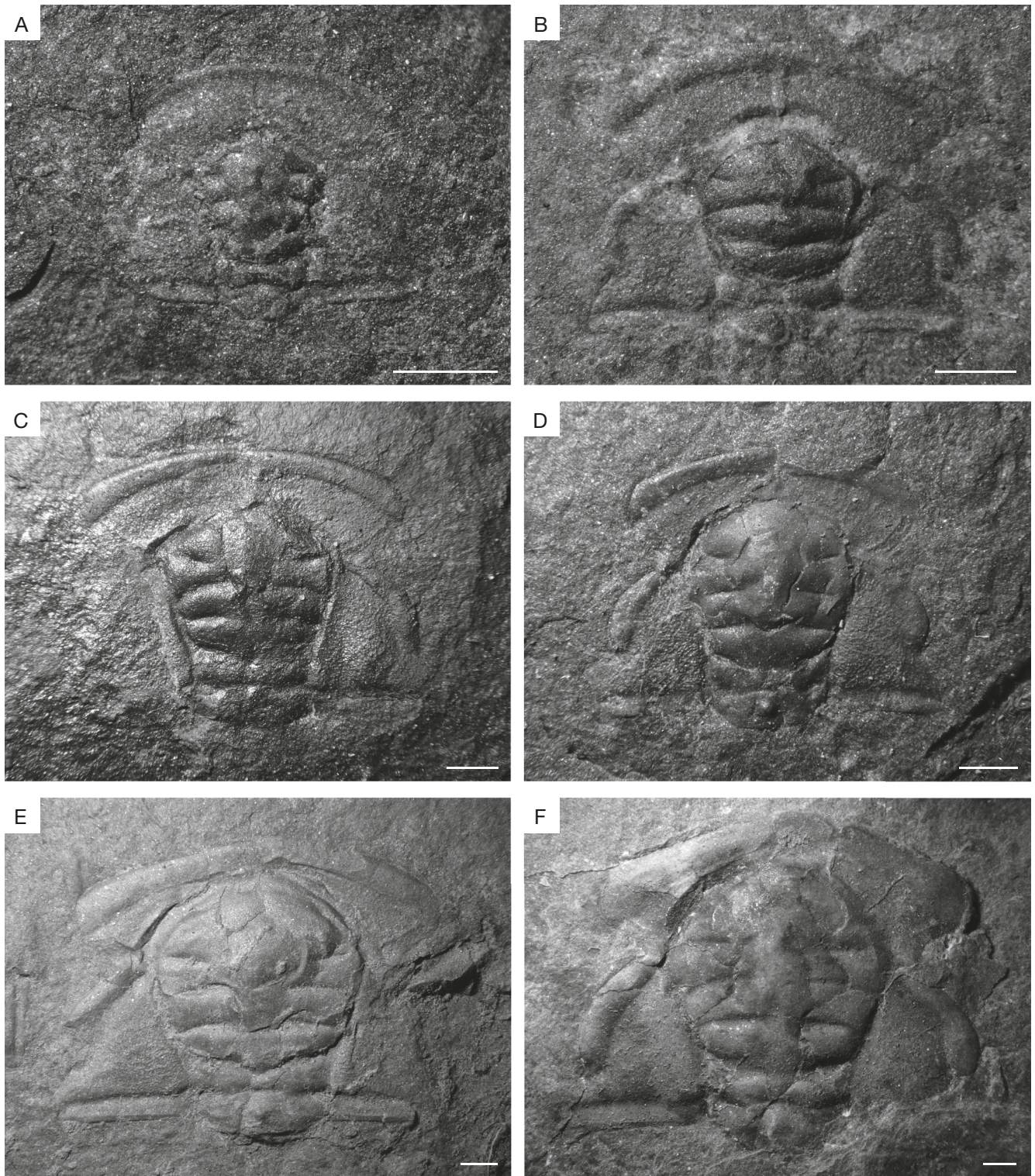


FIG. 14. — *Plutonides hicksii* (Salter, 1866b): **A**, internal cast of a juvenile cranidium, smallest described specimen in this work with long preglabellar field (NFM F-3177 from 10.27 m); **B**, internal cast of a juvenile cranidium, deep glabellar furrows, ornamentation on fixigenae preserved (NFM F-3220 from 7.59 m); **C**, internal cast of a juvenile cranidium, deep glabellar furrows (NFM F-3026 from 9.63 m); **D**, internal cast of a juvenile cranidium, with occipital node and ornamentation on fixigenae preserved (NFM F-3176 from 10.27 m); **E**, internal cast of a juvenile cranidium, short preglabellar field, occipital node preserved (NFM F-3067 from 3.33 m); **F**, internal cast of a juvenile cranidium, short preglabellar field, glabellar furrows less deeply impressed than in younger specimens A-D, S2 furrow shallower axial to discontinuous (NFM F-3947 from 4.28 m). Scale bars: 1 mm.

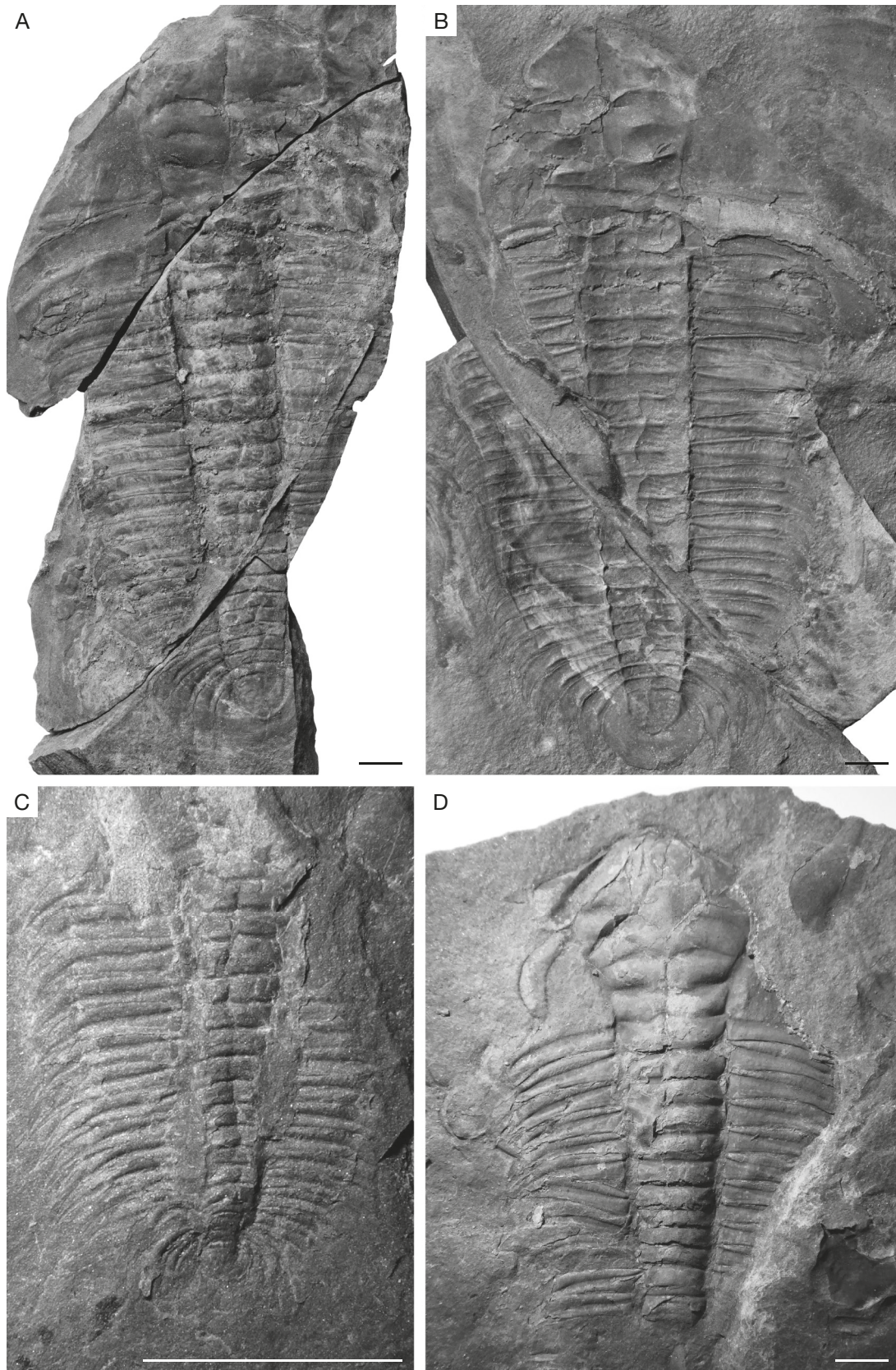


FIG. 15. — *Plutonides hicksii* (Salter, 1866b): **A**, internal cast of a cranidium, occipital node preserved, with a vertical groove crossing the cranidium (NFM F-2781 from 4.52 m); **B**, internal cast of a cranidium with preserved exoskeleton (NFM F-3894 from 2.96 m); **C**, internal cast of a cranidium, occipital node and ornamentation on fixigenae preserved (NFM F-2861 from 2.53); **D**, internal cast of a cranidium, with a vertical groove crossing the cranidium (NFM F-3258 from 4.06 m). Scale bar: 3 mm.

HOLOTYPE. — Specimen no. BGS(GSM) 10113, British Geological Survey, London, United Kingdom by original designation, from the Clogau Formation, Menevian Group of the Mawddach valley, Gwynedd, Wales, United Kingdom.

DIAGNOSIS. — S1 shallowing and curving backwards axially, S2 and S3 curving forward, S3 and S4 short, all well-defined; occipital ring broadens axially; pygidium nearly circular in outline with wide axis ending in a blunt point at about half pygidial length (based on Lake 1934, 1935; Fletcher 1972b, with modifications).

MATERIAL EXAMINED. — 101 cranidia and 21 pygidia of *Plutonides hicksii* (for NFM numbers see Appendix 1). All specimens range between 1.96 and 10.37 m (Fig. 2) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

OCCURRENCE. — *Plutonides hicksii* is a regional biostratigraphical marker for the middle Cambrian (Howell 1925; Lake 1935; Hutchinson 1962) and has been documented from southeastern Canada, eastern Newfoundland, in the *Paradoxides hicksii* and *Paradoxides davidis* zones (Hutchinson 1962; Whittington *et al.* 1997; Fletcher 2006, 2007). Further occurrences are in southeastern Canada in Nova Scotia (Hutchinson 1952), United Kingdom in Wales (*Ptychagnostus gibbus* to *Tomagnostus fissus* zones; Salter & Hicks 1869; Lake 1934; Thomas *et al.* 1984; Whittington *et al.* 1997) and England (*Ptychagnostus gibbus* to *Tomagnostus fissus* zones; Cobbold 1913; Thomas *et al.* 1984; Bridge *et al.* 1998), Denmark (*Acidusus atavus* Zone; Grönwall 1902; Weidner & Nielsen 2014) and Sweden (*Tomagnostus fissus* and *Ptychagnostus atavus* zones; Linnarsson 1879, 1882; Westergård 1953).

DESCRIPTION

The cranidia range from 3.0 mm to 51.0 mm width and from 2.5 mm to 41.0 mm length. The width of the pygidia varies from 5.0 to 28.0 mm and from 4.0 mm to 24.0 mm in length. Both cranidia and pygidia are well-preserved as internal casts and moulds. Some cranidial internal cast have a groove running from the frontal margin across the glabella towards the outer margin of the middle of the occipital ring. In at least two thirds of the specimens, the occipital ring bears a small node. On the cranidia, the finely reticulate, ridged surface ornamentation is best preserved on the genae. In smaller specimens, the glabellar furrows are more deeply impressed, with S2 almost transglabellar. The glabella is short with a long preglabellar field towards the outer margin. The glabella in the anterior third is more domed than in bigger specimens. In specimens with an occipital ring, the latter also bears a small node.

REMARKS

Plutonides hicksii has been assigned to different genera (e.g., Fletcher 1972b, 2007; Whittington *et al.* 1997; Geyer *et al.* 2022). It was first described as *Paradoxides*, but this assignment is outdated as discussed above (see remarks *Plutonides*). Šnajdr (1958) assigned *Hydrocephalus hicksii hicksii* as a species within the genus *Hydrocephalus* without further discussion. Later, Fletcher (1972b) reported the species as *Hydrocephalus hicksii*, followed by Martin & Dean (1988) who assigned it to *Paradoxides* (*Hydrocephalus*) *hicksii*, but no discussion was presented by the authors. According to the diagnosis for the genus *Hydrocephalus*, given by Šnajdr (1958) and Whittington *et al.* (1997), the genus is characterized by a

transglabellar S2 furrow, a subcircular glabellar front, short palpebral lobes not extending to close towards the posterior margin, and a posterior margin curving forward to an acute inner spine angle. These characteristics do not match *Pl. hicksii*. Whittington *et al.* (1997) mentioned that supposed examples described as the genus *Hydrocephalus*, from eastern Canada are referred to *Plutonides*. Morris (1988) marked the generic reference of ‘*Paradoxides*’ *hicksii* as provisional, pointing out the problem of the generic ranking of the species. Fletcher (2007) rejected the assignment of *Pl. hicksii* to *Plutonides* as done by Whittington *et al.* (1997). He referred to Fletcher *et al.* (2005), who described the cranidium of *Acadoparadoxides* as indistinguishable from *Plutonides*. He based his argument on a reconstructed photograph of the distorted lectotype of the type species of *Plutonion sedgwickii* Hicks, 1871. The image shows a small-sized specimen with deep, transglabellar S1 and S2 furrows, a rounded glabellar front and relatively long palpebral lobes. The bigger cranidia of the type species of *Plutonides* figured by Fletcher *et al.* (2005) have an S2 furrow that shallows axially to a degree in which they are not transglabellar any more, and palpebral lobes reaching from S1 to L1. These characteristics differ from the characteristics given for *Acadoparadoxides*, e.g., a transglabellar S2 furrow, long palpebral lobes reaching from L0 to the posterior marginal furrow (Šnajdr 1958; Whittington *et al.* 1997). The assignment of *Plutonides* as a senior synonym of *Acadoparadoxides* as done by Fletcher *et al.* (2005) is not followed here. Rather, we follow the assignment of the species *Pl. hicksii* to the genus *Plutonides* as done by e.g., Whittington *et al.* (1997) and Young *et al.* (2002). Whittington *et al.* (1997) described the meraspis stage of *Plutonides* and documented a short frontal lobe, a long preglabellar field, and deep glabellar furrows. All these characteristics are present in small-sized specimens of *Pl. hicksii* in this work (e.g., NFM F-3177, NFM F-3220, NFM F-3026). It is noteworthy that various authors (e.g., Cobbold 1913; Lake 1934, 1935; Egorova *et al.* 1982; Bushuev & Makarova 2016) have referred to *Pl. hicksii* as “*Pl. hicksi*”, with no further discussion.

Paradoxides hicksii var. *palpebrosus* described by Linnarsson (1879) matches *Pl. hicksii* and is here taken as a synonym of *Pl. hicksii*. Lake (1934: fig. 4) figured a hypostome, and Hutchinson (1952: pl. 2, fig. 5) a fragmentary librigena, but these assignments are questionable. This is also the case for two cranidia illustrated in Fletcher (1972b: pl. 47, fig. 15 and pl. 48, fig. 2) which are poorly preserved, both with a deep crack crossing the specimens. Cranidia figured by Vaněk *et al.* (1999: pl. 1, figs 1-3, 5, 6) have transglabellar S1 and S2 furrows and no S3 or S4 furrow. The glabellar furrows do not match the characteristic four furrows of *Pl. hicksii*. Vaněk *et al.*’s plate 1, figure 3 only shows a hypostome and plate 1, figure 4, illustrates a pygidium. Both pictures have a poor resolution and the pygidium appears to be elongate and not as rounded as in *Pl. hicksii*. Consequently, all illustrated specimens are excluded from *Pl. hicksii*. Instead, their characteristics match *Pa. davidis* and specimens illustrated on plate 1, figures 1-6, are assigned to this species.

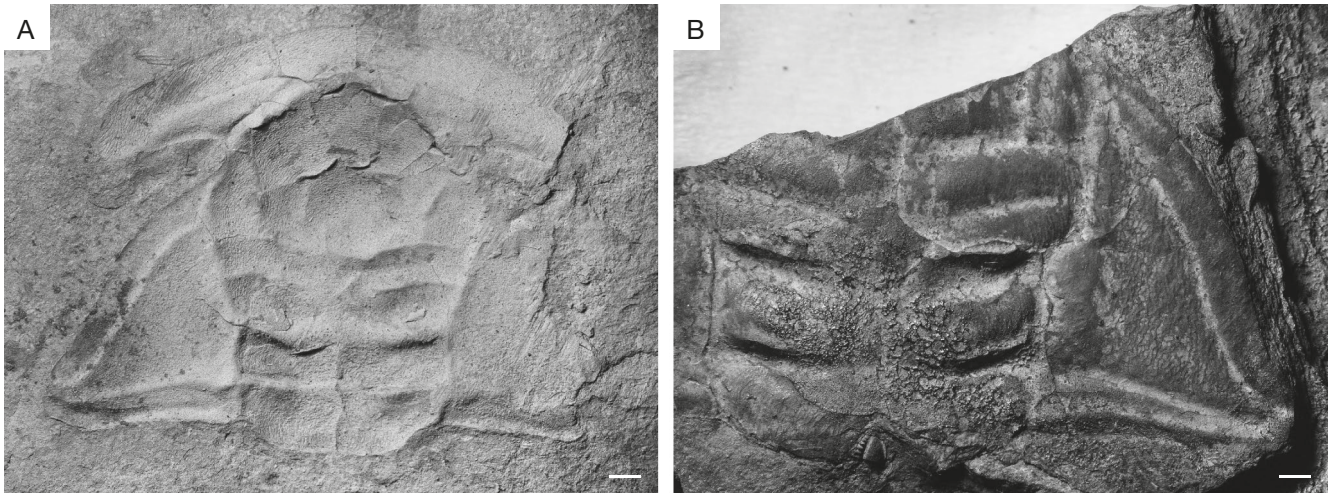


FIG. 16. — *Clarella venusta* (Billings, 1872): **A**, mould of a cranidium (NFM F-3096 from 16.25 m); **B**, disarticulated internal cast of a cranidium (NFM F-3548 from 16.25 m). Scale bar: 1 mm.

Family CENTROPLEURIDAE Angelin, 1854

Genus *Clarella* Howell, 1933

Clarella Howell, 1933: 219. — Type species: *Anapolenus venustus* Billings, 1872, designated as lectotype by Howell (1933).

DIAGNOSIS. — Glabella with great forward expansion anterior of S1; palpebral lobes slightly sigmoidal, reaching almost genal angle; thorax with 15 segments; pygidium without border, up to four pairs of marginal spines; short axis with one to two axial rings (based on Howell 1933; Whittington *et al.* 1997, with modifications).

REMARKS

Clarella is distinguished from *Anapolenus* Salter, 1864a by sigmoidally shaped palpebral lobes that almost reach the genal angle. The palpebral lobes of *Anapolenus* curve in a uniform arc, reaching the genal angle. The pygidium of *Clarella* lacks a border, while that of *Anapolenus* is bordered (Howell 1933; Whittington *et al.* 1997).

Clarella venusta (Billings, 1872) (Fig. 16)

Anapolenus venustus Billings, 1872: 474–476, fig. 11; 1874: 73, 74, fig. 42.

Clarella venusta – Hutchinson 1962: 111, 112, pl. 17, figs 7–10. — Martin & Dean 1988: 19, pl. 1, fig. 13. — Whittington *et al.* 1997: figs 308.1a, b. — Fletcher 2006: pl. 34, fig. 11 (*partim*).

LECTOTYPE. — Specimen GSC No. 284a, Geological Survey of Canada, Ottawa, Canada, designated as lectotype by Whittington *et al.* (1997). From Chapel Arm, Trinity Bay, Newfoundland, Canada.

DIAGNOSIS. — Glabella not reaching anterior margin; L4 short; eye lobes from L1 to S4; pygidium with two pairs of short marginal spines.

MATERIAL EXAMINED. — Three cranidia of *Clarella venusta* (NFM F-3069; NFM F-3548; NFM F-3657). All specimens range between

16.25 and 16.27 m (Fig. 2) within the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

OCCURRENCE. — *Clarella venusta* is rare in the middle Cambrian and only reported from southeastern Canada, eastern Newfoundland, in the *Paradoxides hicksi* and *Paradoxides davidis* zones (Hutchinson 1962; Martin & Dean 1988; Fletcher 2006).

DESCRIPTION

The cranidium (NFM F-3096) is 22.2 mm in width and 15.8 mm in length. The width of the glabella is 10.3 mm and the length is 10.8 mm. Due to the preservation of NFM F-3548; NFM F-3657 a solid measurement was not possible. The three cranidia are preserved as one disarticulated internal cast and two moulds.

REMARKS

The cranidium of *Clarella venusta* is similar to *Clarella impar* (Hicks, 1872). The palpebral lobes of *C. venusta* are narrower and curved more sigmoidally than those of *C. impar* (Cook, 1997). The librigena illustrated by Fletcher (2006: pl. 34, fig. 12) is disarticulated and its suture of the librigena does not match that of *C. venusta*. It is here excluded from the species.

Order CORYNEXOCHIDA Kobayashi, 1935

Family CORYNEXOCHIDAE Angelin, 1854

Subfamily ACOTHEINAE Westergård, 1950

Genus *Acontheus* Angelin, 1851

Acontheus Angelin, 1851: 5. — Type species: *Acontheus acutangulus* Angelin, 1851, by original designation.

Aneucanthus – Angelin 1851: X.

Aneucanthus – Barrande 1857: 17.

DIAGNOSIS. — Cranidium with narrow margin; glabella expands anteriorly, extends to anterior margin; pygidium subelliptical; pygidial axis of three or four axial rings, not reaching pygidial margin; wide pleural furrows extend to border with marked posterior deflection (based on Angelin 1851; Jago *et al.* 2012, with modifications).

REMARKS

Angelin (1851) first described the genus *Acontheus* and renamed it in the same publication. He introduced the name *Aneucanthus* for the genus, but as this was preoccupied by the name of a snake, he renamed the trilobite *Aconthias*. Barrande (1857) used *Aneucanthus* for the genus, which was also used by Lindström in the second edition of Angelin's (1851) work that was revised and published as Angelin (1878). We suggest that *Aneucanthus* was incorrectly spelled as Barrande (1857) used the name without any further discussion or explanation. According to Westergård (1950: 8) *Acontheus* can be distinguished from *Aconthias* and therefore the original name *Acontheus* is used herein.

Acontheus inarmatus Hutchinson, 1962 (Fig. 17)

Acontheus inarmatus Hutchinson, 1962: 109, pl. 16, figs 8a, b, 9.

Acontheus inarmatus minutus Sdzuy, 2000: 307, pl. 3, figs 1-5 (*partim*). — Geyer 2010: unnamed plate p. 84, fig. 7. — Heuse *et al.* 2010: fig. 4.16.

HOLOTYPE. — Specimen no. GSC No. 12053, Geological Survey of Canada, Ottawa, Canada, by original designation, from the Manuels River Formation on the north shore of Highland Cove, Trinity Bay, Newfoundland, Canada.

DIAGNOSIS. — Glabella expands anteriorly up to three times wider than posterior part; faint glabellar furrows; rounded, inflated fixiginae; rounded genal angle; punctuate exoskeleton.

MATERIAL EXAMINED. — 14 cranidia of *Acontheus inarmatus* (for NFM numbers see Appendix 1). All specimens range between 15.63 and 16.67 m (Fig. 2) of the Manuels River Formation, type locality, Conception Bay South, Newfoundland, Canada.

OCCURRENCE. — *Acontheus inarmatus* is a rare middle Cambrian taxon, reported from southeastern Canada, eastern Newfoundland, in the *Paradoxides davidis* Zone (Hutchinson 1962). It has further been documented from Germany (Sdzuy 2000).

DESCRIPTION

The cranidia range from 1.4 mm to 4.1 mm in width and from 1.3 mm to 3.9 mm in length. The cranidia are well-preserved as internal casts and moulds. The glabella is more domed than the cheeks and glabellar furrows are faintly preserved in two specimens (NFM F-3143 and NFM F-3659). The specimens have a smooth to slightly punctuate surface and none has the exoskeleton preserved. Two specimens bear an occipital node (NFM F-3211 and NFM F-3701) and three are pyritized.

REMARKS

Sdzuy (2000) introduced *Acontheus inarmatus minutus* based on a smoother exoskeleton than in Hutchinson's (1962) specimens and a slightly differing occipital ring. Sdzuy (2000)

acknowledged that these differences in eight cranidia and one pygidium, may have resulted from poor preservation of his specimens. We also refer to these differences as preservational and the result of intraspecific variation and assign *Ac. inarmatus minutus* as a synonym. The pygidium figured by Sdzuy (2000: pl. 3, fig. 6) does not match the characteristics of *Acontheus* and is here excluded from the genus. Geyer (2010) and Heuse *et al.* (2010) followed Sdzuy (2000) in applying the subspecies and illustrated both one of Sdzuy's (2000) cranidia. The cranidia show the characteristics of *Ac. inarmatus*, so the specimens are here assigned to the species.

BIOSTRATIGRAPHY

Early studies on the Manuels River Formation mixed lithostratigraphic and biostratigraphic concepts and misleading terms were introduced such as “Paradoxides Beds in the upper part” (Murray 1869), “Horizon of *Paradoxides davidis*” (Matthew 1886), or “Subzone of *Paradoxides davidis*” (Matthew 1896). The first detailed bed-by-bed study of the Manuels River Formation was done by Howell (1925). This author also introduced the *Paradoxides hicksi* and *Paradoxides davidis* zones within today's Manuels River Formation using these to define formations. Hutchinson (1962) applied Howell's (1925) biozonation. Later, Martin & Dean (1988) studied trilobites and acritarches. They redefined the older zonation and introduced three biozones based on agnostids, the *Tomagnostus fissus* and *Ptychagnostus atavus* Zone, the *Hypagnostus parvifrons* and the *Ptychagnostus punctuosus* zones. With the most recent study by Hildenbrand *et al.* (2021) four interval biozones based on the contained agnostid trilobites were introduced (from base to top): the *Tomagnostus fissus* Zone, the *Hypagnostus parvifrons* Zone, the *Ptychagnostus atavus* Zone and the *Ptychagnostus punctuosus* Zone (Fig. 2). This biozonal division based on agnostid trilobites is here maintained but supplemented and refined by the ranges of polymerid trilobites (Fig. 2).

TOMAGNOSTUS FISSUS ZONE

Polymerids are most abundant and diverse in this basal zone of the Manuels River section (478 specimens, 7 out of 10 described species). *Agraulos ceticephalus* first appears abundantly (first occurrence; FO) at 1.94 m of the section and is common to abundant in the section to its last occurrence (LO) at 9.11 m. Below the *T. fissus* Zone 204 specimens of *Ag. ceticephalus* occur within an acme of c. 1 m range between 1.94 m and 3.11 m of the section. *Plutonides hicksii* first occurs at 1.96 m and is rare to common within the *T. fissus* Zone up to its LO at 10.37 m. The FO of *Jincella? appplanata* is at 4.44 m of the section. This species is rare in the decimeters above the FO but increasingly abundant towards the top of the *T. fissus* Zone. A single specimen of *Bailiella aequalis* was identified at 5.90 m within this Zone. *Bailiella tenuicincta* is a rare taxon which first occurs at 8.52 m. *Paradoxides davidis* and *Meneviella venulosa* are also rare and first occur at 9.56 m and 10.00 m, respectively.

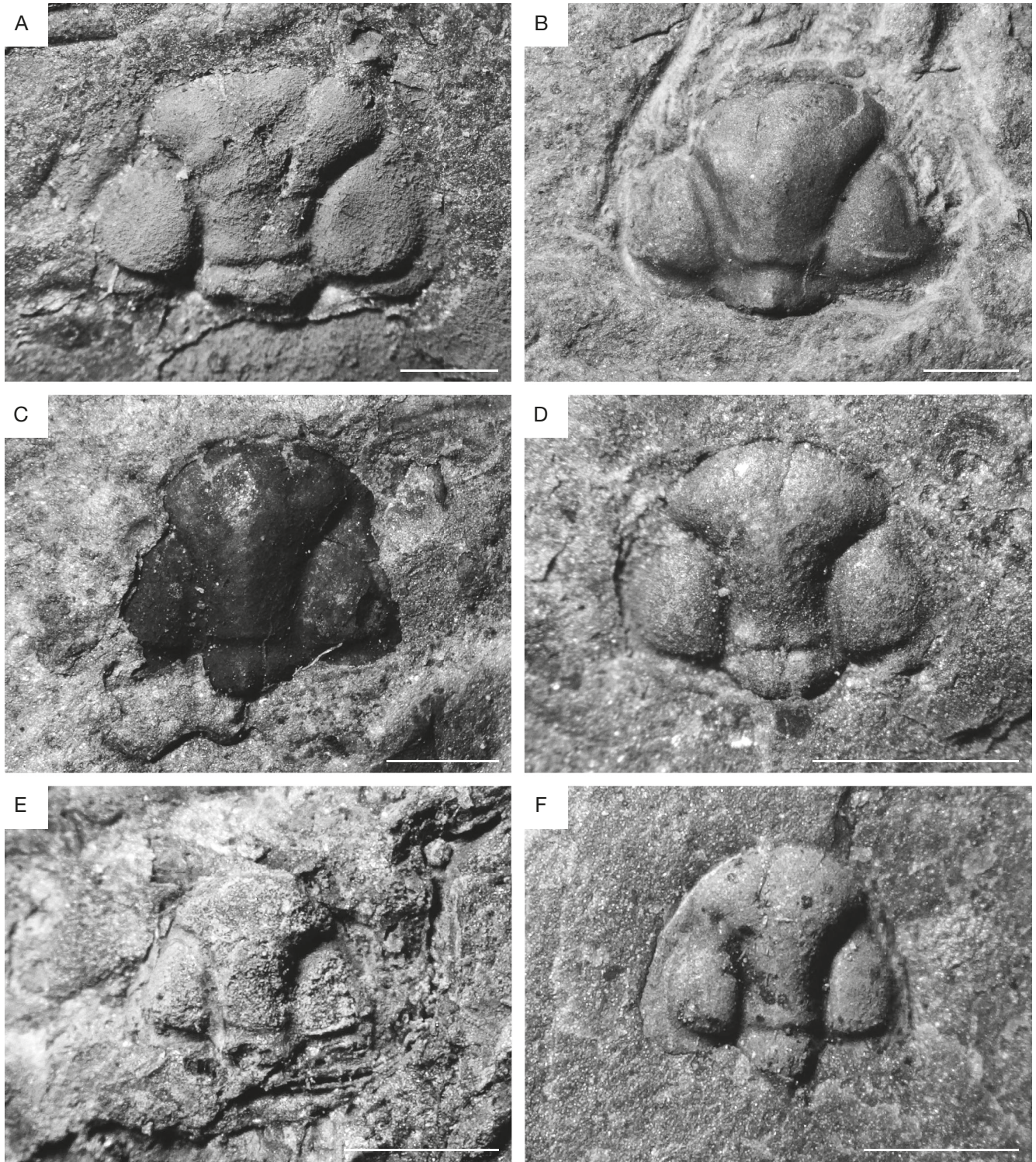


FIG. 17. — *Acontheus inarmatus* Hutchinson, 1962: **A**, internal cast of a cranidium, faint glabellar furrows preserved, slightly punctuated ornamentation (NFM F-3143 from 16.67 m); **B**, internal cast of a cranidium, occipital node preserved (NFM F-3211 from 15.63 m); **C**, internal cast of a cranidium, occipital node preserved (NFM F-3701 from 15.68 m); **D**, internal cast of a cranidium, slightly punctuated ornamentation (NFM F-3150 from 16.67 m); **E**, internal cast of a cranidium (NFM F-3167 from 16.67 m); **F**, internal cast of a cranidium, glabellar furrows on left side of glabella slightly visible (NFM F-3659 from 16.67 m). Scale bars: 1 mm.

HYPAGNOSTUS PARVIFRONS ZONE

Towards the top of the *H. parvifrons* Zone *Paradoxides davidis* is very abundant (48 specimens) between 11.66 and

11.90 m of the Manuels River section. Other polymerids are notably absent, even though *J.?* *applanata*, *B. tenuicincta* and *M. venulosa* appear beneath and above this zone.

PTYCHAGNOSTUS ATAVUS ZONE

Jincella? applanata is a rare taxon in the lower half of the zone but it increases in abundance in the upper part and reaches very high abundance close to the LO of the species at 16.67 m. *Bailiella tenuicincta* is rare at its LO also at 16.67 m. *Paradoxides davidis* is very abundant at the bottom of the *Pt. atavus* Zone and is rare to common throughout the zone. *Meneviella venulosa* is common between 15.68 m and 15.76 m and rare above to its LO at 16.55 m. A single specimen of *Sao hirsuta* was identified at 15.68 m and thus close to the top of the *Pt. atavus* zone. *Acontheus inarmatus* occurs commonly from its FO at 15.63 m to LO at 16.67 m, while *Clarella venusta* is another rare species ranging from its FO at 16.25 m to LO at 16.27 m of the Manuels River section.

PTYCHAGNOSTUS PUNCTUOSUS ZONE

Paradoxides davidis is the only polymerid described from the zone. It is a rare to common taxon with a LO at 17.89 m. Hildenbrand *et al.* (2021) noted that the top of the *Pt. punctuosus* zone is not within the Manuels River Formation but in the not yet formally defined Elliot Cove formation (Fig. 2).

DISCUSSION

The collection of Howell (1925) is considered lost (Hildenbrand *et al.* 2021) and there are no taxonomic descriptions and photographic images of most of the taxa reported by Howell (1925), making it difficult to reproduce his taxonomic work. However, the biozones introduced by Howell (1925) appear to be applicable and were used here. Howell (1925) defined the base of the *Paradoxides hicksi* Zone at his bed 36, which corresponds to the base of the Manuels River Formation as defined by Hutchinson (1962). *Plutonides hicksii* is here first described at the 1.96 m level of the section, and is thus present above Howell's (1925) FO of *Pl. hicksii*. According to Austermann (2016) the FO of *Paradoxides davidis* in bed 93 (Howell 1925) corresponds to the 9.56 m level used here for the FO of the taxon. The FO of *Pa. davidis* as established by Howell (1925) thus corresponds to the FO as identified here, thus allowing for accurate correlations of Howell's (1925) work with the agnostid interval biozones introduced by Hildenbrand *et al.* (2021), to which we here refer to.

TOMAGNOSTUS FISSUS ZONE

Hildenbrand *et al.* (2021) established this zone as a local interval biozone. The *T. fissus* Zone is correlated with the upper part of the *Pa. hicksi* Zone and the lower 1.4 m of the *Pa. davidis* Zone as introduced by Howell (1925). *Pl. hicksii* is further known from the *T. fissus* Zones of the United Kingdom (Thomas *et al.* 1984) and Sweden (Westergård 1953). Howell (1925) did not mention *Agraulos ceticephalus* but described *Agraulos socialis* (Billings, 1872) within the *Pa. hicksi* Zone, but no systematic work and illustrations were presented by the author. We suggest that Howell (1925) misinterpreted the species. Our interpretation is based on the fact that the range of *Ag. socialis* roughly correlates with our range of *Ag.*

ceticephalus. In addition, specimens of *Ag. socialis* previously described by Fletcher (2017) from Newfoundland, are here identified as *Ag. ceticephalus*. We here report a single occurrence of *B. aequalis* within this Zone. The species is further known from the *Pt. punctuosus* Zone from Sweden (Westergård 1953) and Denmark (Rudolph 1994).

HYPAGNOSTUS PARVIFRONS ZONE

The zone correlates with the lower part of the *Pa. davidis* Zone as introduced by Howell (1925). The *Hypagnostus parvifrons* Zone lacks polymerid trilobites except for *Pa. davidis* which shows acme abundance near the upper zonal boundary.

PTYCHAGNOSTUS ATAVUS ZONE

The zone correlates with the middle part of the *Pa. davidis* Zone as introduced by Howell (1925). Hildenbrand *et al.* (2021) documented abundant agnostid trilobites from this Zone, in particular from levels rare in polymerids. It is remarkable that the LOs of *J. applanata*, *B. tenuicincta*, *M. venulosa*, and *Ac. inarmatus* are all close to the top of the *Pt. atavus* Zone. Within the zone *Sao hirsuta* is here reported. This is the first occurrence of the taxon from Avalonia. Elsewhere, the species is well known from the *Eccaparadoxides pusillus* Zone of the Czech Republic (Šnajdr 1958). *Clarella venusta* was described from this zone and is further only known from the *Pa. hicksi* Zone of Newfoundland (Hutchinson 1962; Fletcher 2006).

PTYCHAGNOSTUS PUNCTUOSUS ZONE

The zone correlates with the upper *Pa. davidis* Zone as introduced by Howell (1925). *Pa. davidis* is the only polymerid trilobite species reported here from this zone. Hildenbrand *et al.* (2021) also remarked on the occurrence of only one agnostid species in this zone. As only two trilobite species (*Pt. punctuosus* and *Pa. davidis*) are reported from this zone (also see Hildenbrand *et al.* 2021), trilobite diversity must have decreased substantially compared to the zones below. The occurrence of *Pa. davidis* presented here matches with the range in Howell (1925). *Paradoxides davidis* is further known from the *Pt. punctuosus* Zone of Sweden (Westergård 1953). Howell (1925) also reported *Paradoxides rugulosus* Hawle & Corda, 1847; *Centropleura henrici* (Salter, 1864a); *Solenopleuropsis (Solenopleura) variolaris* (Salter, 1864a); *Solenopleura communis* (Billings, 1874); *Holocephalina primordialis* Salter, 1864a; and *Corynexochus minor* (Walcott, 1889), but these taxa were not identified in the present study. As noted above, Howell's (1925) study lacks images and taxonomic descriptions of almost all his taxa, all specimens of which are lost, and the names are here interpreted as dubious.

Polymerid trilobites have commonly been used to define biozones on Avalonia (e.g., Howell 1925; Landing & Westrop 1998a; Fletcher 2006) for historical reasons, their abundance, and due to their significance for regional correlation. More recently, however, agnostid trilobites are increasingly used for the chronostratigraphic division of the middle Cambrian, which is due to their abundant occurrence, their cosmopolitan distribution in open-marine facies and relatively short stratigraphic ranges (Robinson 1984; Peng & Robinson 2000; Hildenbrand

2016; Hildenbrand *et al.* 2021). Based on solid systematic documentation, we here suggest that a use of polymerids and agnostids combined (Fig. 2), provides a new chronostratigraphic tool for solid regional and intercontinental correlation.

CONCLUSION

The Drumian (middle Cambrian, Miaolingian) Manuels River Formation, Newfoundland, Canada comprises a well-preserved assemblage of polymerid trilobites, which is comparable with that of other parts of Avalonia, but also Baltica and even Gondwana. The *Pa. davidis* and *Pa. hicksi* zones are widely used on Avalonia and can be well correlated with established agnostid biozones, i.e. (from base to top) the *Tomagnostus fissus*, *Hypagnostus parvifrons*, *Ptychagnostus atavus*, and *Ptychagnostus punctuosus* zones. Agnostida are majorly used today for biostratigraphic assignment and correlation of the middle Cambrian. Nevertheless, a combination of both polymerid and agnostid trilobites may provide a new opportunity for refined intercontinental correlation of the study area. While *Agraulos ceticephalus*, *Jincella? applanata*, *Bailiella tenuicincta*, *Meneviella venulosa*, *Paradoxides davidis*, *Plutonides hicksii*, *Clarella venusta* and *Acontheus inarmatus* have previously been described from Newfoundland, *Bailiella aequalis* has not been illustrated yet and *Sao hirsuta* is described from eastern Avalonia for the first time. Both, the genus *Agraulos* and the clade of *Paradoxides sensu lato*, are in the need of comprehensive revisions. *Paradoxides* (*Mawddachites*) is here considered to be a synonym of *Plutonides* and *Pl. hicksii* is here assigned to represent the latter genus. *Agraulos* also requires revision and the relationship between *Ag. ceticephalus* and *Ag. longicephalus* cannot be fully resolved.

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Authors contributions

The study is based on fieldwork by AH and GA in 2012 and 2013. The study was designed by TU, AH and GA. Palaeontological interpretations and implications developed from discussions with AH, GA and WS. The manuscript was prepared with input from all co-authors.

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APPENDIX 1. — List of specimen NFM catalogue.

<i>Acontheus inarmatus</i>	NFM F-3143, NFM F-3144, NFM F-3150, NFM F-3151, NFM F-3167, NFM F-3211, NFM F-3417, NFM F-3418, NFM F-3659, NFM F-3660, NFM F-3693, NFM F-3701, NFM F-3707, NFM F-3708.	NFM F-3221, NFM F-3222, NFM F-3223, NFM F-3224, NFM F-3225, NFM F-3226, NFM F-3229, NFM F-3233, NFM F-3234, NFM F-3235, NFM F-3240, NFM F-3242, NFM F-3245, NFM F-3250, NFM F-3251, NFM F-3254, NFM F-3255, NFM F-3256, NFM F-3257, NFM F-3260, NFM F-3261, NFM F-3262, NFM F-3263, NFM F-3264, NFM F-3265, NFM F-3266, NFM F-3267, NFM F-3268, NFM F-3269, NFM F-3270, NFM F-3271, NFM F-3273, NFM F-3274, NFM F-3275, NFM F-3276, NFM F-3277, NFM F-3278, NFM F-3279, NFM F-3280, NFM F-3281, NFM F-3284, NFM F-3285, NFM F-3287, NFM F-3288, NFM F-3289, NFM F-3290, NFM F-3291, NFM F-3293, NFM F-3294, NFM F-3295, NFM F-3296, NFM F-3298, NFM F-3305, NFM F-3306, NFM F-3307, NFM F-3310, NFM F-3313, NFM F-3314, NFM F-3315, NFM F-3316, NFM F-3317, NFM F-3318, NFM F-3319, NFM F-3321, NFM F-3322, NFM F-3330, NFM F-3331, NFM F-3332, NFM F-3333, NFM F-3341, NFM F-3344, NFM F-3345, NFM F-3346, NFM F-3348, NFM F-3349, NFM F-3351, NFM F-3355, NFM F-3356, NFM F-3357, NFM F-3359, NFM F-3363, NFM F-3365, NFM F-3369, NFM F-3371, NFM F-3372, NFM F-3373, NFM F-3381, NFM F-3383, NFM F-3384, NFM F-3385, NFM F-3386, NFM F-3387, NFM F-3388, NFM F-3389, NFM F-3390, NFM F-3391, NFM F-3392, NFM F-3393, NFM F-3394, NFM F-3395, NFM F-3396, NFM F-3397, NFM F-3434, NFM F-3435, NFM F-3436, NFM F-3437, NFM F-3438, NFM F-3439, NFM F-3440, NFM F-3443, NFM F-3447, NFM F-3449, NFM F-3451, NFM F-3456, NFM F-3457, NFM F-3458, NFM F-3459, NFM F-3463, NFM F-3464, NFM F-3465, NFM F-3466, NFM F-3467, NFM F-3468, NFM F-3469, NFM F-3470, NFM F-3471, NFM F-3472, NFM F-3473, NFM F-3474, NFM F-3476, NFM F-3477, NFM F-3478, NFM F-3479, NFM F-3480, NFM F-3481, NFM F-3482, NFM F-3483, NFM F-3484, NFM F-3485, NFM F-3486, NFM F-3487, NFM F-3488, NFM F-3489, NFM F-3490, NFM F-3491, NFM F-3492, NFM F-3493, NFM F-3494, NFM F-3497, NFM F-3498, NFM F-3499, NFM F-3500, NFM F-3501, NFM F-3502, NFM F-3503, NFM F-3504, NFM F-3505, NFM F-3506, NFM F-3507, NFM F-3508, NFM F-3509, NFM F-3510, NFM F-3511, NFM F-3512, NFM F-3513, NFM F-3514, NFM F-3515, NFM F-3516, NFM F-3517, NFM F-3518, NFM F-3519, NFM F-3520, NFM F-3521, NFM F-3522, NFM F-3523, NFM F-3524, NFM F-3525, NFM F-3621, NFM F-3668, NFM F-3725, NFM F-3745, NFM F-3746, NFM F-3748, NFM F-3749, NFM F-3750, NFM F-3751, NFM F-3752, NFM F-3753, NFM F-3754, NFM F-3755, NFM F-3756, NFM F-3757, NFM F-3758, NFM F-3759, NFM F-3762, NFM F-3763, NFM F-3764, NFM F-3765, NFM F-3766, NFM F-3767, NFM F-3768, NFM F-3769, NFM F-3770, NFM F-3771, NFM F-3772, NFM F-3773, NFM F-3774, NFM F-3775, NFM F-3776, NFM F-3777, NFM F-3778, NFM F-3779, NFM F-3780, NFM F-3782, NFM F-3783, NFM F-3784,
<i>Agraulos ceticephalus</i>	NFM F-2779, NFM F-2780, NFM F-2785, NFM F-2786, NFM F-2787, NFM F-2788, NFM F-2790, NFM F-2791, NFM F-2797, NFM F-2798, NFM F-2799, NFM F-2800, NFM F-2801, NFM F-2802, NFM F-2803, NFM F-2804, NFM F-2807, NFM F-2808, NFM F-2809, NFM F-2810, NFM F-2811, NFM F-2812, NFM F-2834, NFM F-2835, NFM F-2836, NFM F-2837, NFM F-2838, NFM F-2839, NFM F-2850, NFM F-2851, NFM F-2852, NFM F-2853, NFM F-2854, NFM F-2855, NFM F-2856, NFM F-2857, NFM F-2858, NFM F-2859, NFM F-2860, NFM F-2862, NFM F-2863, NFM F-2864, NFM F-2865, NFM F-2866, NFM F-2867, NFM F-2868, NFM F-2869, NFM F-2870, NFM F-2871, NFM F-2872, NFM F-2873, NFM F-2874, NFM F-2875, NFM F-2876, NFM F-2877, NFM F-2879, NFM F-2880, NFM F-2881, NFM F-2882, NFM F-2883, NFM F-2884, NFM F-2885, NFM F-2886, NFM F-2887, NFM F-2888, NFM F-2889, NFM F-2900, NFM F-2901, NFM F-2902, NFM F-2903, NFM F-2904, NFM F-2905, NFM F-2906, NFM F-2907, NFM F-2908, NFM F-2909, NFM F-2910, NFM F-2911, NFM F-2912, NFM F-2913, NFM F-2914, NFM F-2915, NFM F-2916, NFM F-2917, NFM F-2918, NFM F-2919, NFM F-2920, NFM F-2921, NFM F-2922, NFM F-2923, NFM F-2924, NFM F-2925, NFM F-2926, NFM F-2927, NFM F-2928, NFM F-2929, NFM F-2931, NFM F-2932, NFM F-2933, NFM F-2935, NFM F-2936, NFM F-2937, NFM F-2938, NFM F-2939.	
<i>Agraulos ceticephalus</i>	NFM F-2945, NFM F-2946, NFM F-2947, NFM F-2948, NFM F-2950, NFM F-2951, NFM F-2952, NFM F-2953, NFM F-2954, NFM F-2955, NFM F-2956, NFM F-2957, NFM F-2958, NFM F-2959, NFM F-2960, NFM F-2961, NFM F-2962, NFM F-2963, NFM F-2966, NFM F-2967, NFM F-2968, NFM F-2969, NFM F-2973, NFM F-2974, NFM F-2983, NFM F-2984, NFM F-2985, NFM F-2986, NFM F-2987, NFM F-2989, NFM F-2990, NFM F-2991, NFM F-3007, NFM F-3029, NFM F-3034, NFM F-3035, NFM F-3037, NFM F-3038, NFM F-3039, NFM F-3040, NFM F-3041, NFM F-3042, NFM F-3043, NFM F-3044, NFM F-3045, NFM F-3046, NFM F-3049, NFM F-3050, NFM F-3051, NFM F-3052, NFM F-3053, NFM F-3054, NFM F-3055, NFM F-3056, NFM F-3057, NFM F-3058, NFM F-3059, NFM F-3060, NFM F-3061, NFM F-3062, NFM F-3063, NFM F-3064, NFM F-3065, NFM F-3066, NFM F-3068, NFM F-3069, NFM F-3070, NFM F-3071, NFM F-3072, NFM F-3073, NFM F-3074, NFM F-3076, NFM F-3077, NFM F-3079, NFM F-3199, NFM F-3201, NFM F-3202, NFM F-3203, NFM F-3204, NFM F-3205, NFM F-3206, NFM F-3207,	

Appendix 1. — Continuation.

NFM F-3785, NFM F-3786, NFM F-3787, NFM F-3788, NFM F-3789, NFM F-3790, NFM F-3791, NFM F-3792, NFM F-3793, NFM F-3794, NFM F-3795, NFM F-3796, NFM F-3797, NFM F-3798, NFM F-3799, NFM F-3800, NFM F-3801, NFM F-3802, NFM F-3803, NFM F-3804, NFM F-3805, NFM F-3806, NFM F-3807, NFM F-3809, NFM F-3813, NFM F-3814, NFM F-3815, NFM F-3816, NFM F-3817, NFM F-3818, NFM F-3819, NFM F-3820, NFM F-3823, NFM F-3831, NFM F-3832, NFM F-3833, NFM F-3835, NFM F-3843, NFM F-3844, NFM F-3845, NFM F-3846, NFM F-3850, NFM F-3851, NFM F-3852, NFM F-3853, NFM F-3854, NFM F-3855, NFM F-3856, NFM F-3857, NFM F-3858, NFM F-3859, NFM F-3860, NFM F-3861, NFM F-3862, NFM F-3863, NFM F-3864, NFM F-3865, NFM F-3866, NFM F-3867, NFM F-3868, NFM F-3869, NFM F-3870, NFM F-3871, NFM F-3872, NFM F-3873, NFM F-3874, NFM F-3875, NFM F-3876, NFM F-3877, NFM F-3878, NFM F-3881, NFM F-3883, NFM F-3885, NFM F-3886, NFM F-3887, NFM F-3888, NFM F-3889, NFM F-3890, NFM F-3891, NFM F-3892, NFM F-3893, NFM F-3895, NFM F-3946, NFM F-3951, NFM F-3952, NFM F-3953, NFM F-3954, NFM F-3955, NFM F-3956, NFM F-3957, NFM F-3958, NFM F-3959, NFM F-3960, NFM F-3961.	NFM F-3132, NFM F-3133, NFM F-3134, NFM F-3135, NFM F-3136, NFM F-3137, NFM F-3138, NFM F-3139, NFM F-3140, NFM F-3141, NFM F-3142, NFM F-3145, NFM F-3146, NFM F-3147, NFM F-3148, NFM F-3149, NFM F-3152, NFM F-3153, NFM F-3154, NFM F-3155, NFM F-3157, NFM F-3158, NFM F-3159, NFM F-3160, NFM F-3163, NFM F-3164, NFM F-3165, NFM F-3166, NFM F-3181, NFM F-3182, NFM F-3183, NFM F-3184, NFM F-3185, NFM F-3186, NFM F-3187, NFM F-3188, NFM F-3189, NFM F-3192, NFM F-3195, NFM F-3196, NFM F-3197, NFM F-3198, NFM F-3212, NFM F-3215, NFM F-3216, NFM F-3217, NFM F-3218, NFM F-3219, NFM F-3238, NFM F-3297, NFM F-3323, NFM F-3324, NFM F-3325, NFM F-3326, NFM F-3327, NFM F-3328, NFM F-3329, NFM F-3334, NFM F-3335, NFM F-3336, NFM F-3337, NFM F-3338, NFM F-3339, NFM F-3342, NFM F-3343, NFM F-3358, NFM F-3362, NFM F-3375, NFM F-3376, NFM F-3398, NFM F-3401, NFM F-3402, NFM F-3403, NFM F-3404, NFM F-3405, NFM F-3406, NFM F-3407, NFM F-3410, NFM F-3411, NFM F-3412, NFM F-3413, NFM F-3414, NFM F-3415, NFM F-3416, NFM F-3421, NFM F-3422, NFM F-3423, NFM F-3424, NFM F-3425, NFM F-3426, NFM F-3427, NFM F-3428, NFM F-3429, NFM F-3430, NFM F-3431, NFM F-3432, NFM F-3441, NFM F-3442, NFM F-3446, NFM F-3448, NFM F-3453, NFM F-3454, NFM F-3455, NFM F-3531, NFM F-3538, NFM F-3539, NFM F-3540, NFM F-3541, NFM F-3542, NFM F-3543, NFM F-3544, NFM F-3545, NFM F-3546, NFM F-3547, NFM F-3560, NFM F-3561, NFM F-3562, NFM F-3563, NFM F-3564, NFM F-3565, NFM F-3566, NFM F-3567, NFM F-3568, NFM F-3569, NFM F-3570, NFM F-3571, NFM F-3572, NFM F-3573, NFM F-3574, NFM F-3575, NFM F-3578, NFM F-3579, NFM F-3580, NFM F-3581, NFM F-3582, NFM F-3583, NFM F-3584, NFM F-3585, NFM F-3586, NFM F-3587, NFM F-3588, NFM F-3594, NFM F-3595, NFM F-3596, NFM F-3597, NFM F-3598, NFM F-3599, NFM F-3605, NFM F-3606, NFM F-3607, NFM F-3608, NFM F-3609, NFM F-3620, NFM F-3630, NFM F-3634, NFM F-3635, NFM F-3636, NFM F-3637, NFM F-3638, NFM F-3639, NFM F-3640, NFM F-3641, NFM F-3642, NFM F-3647, NFM F-3648, NFM F-3649, NFM F-3650, NFM F-3651, NFM F-3652, NFM F-3653, NFM F-3654, NFM F-3658, NFM F-3677, NFM F-3678, NFM F-3681, NFM F-3682, NFM F-3683, NFM F-3684, NFM F-3685, NFM F-3686, NFM F-3687, NFM F-3688, NFM F-3689, NFM F-3690, NFM F-3691, NFM F-3692, NFM F-3694, NFM F-3695, NFM F-3696, NFM F-3697, NFM F-3698, NFM F-3699, NFM F-3703, NFM F-3704, NFM F-3705, NFM F-3706, NFM F-3709, NFM F-3710, NFM F-3711, NFM F-3712, NFM F-3713, NFM F-3714, NFM F-3715, NFM F-3718, NFM F-3719, NFM F-3720, NFM F-3721, NFM F-3722, NFM F-3723, NFM F-3724, NFM F-3726, NFM F-3727, NFM F-3728, NFM F-3729, NFM F-3730, NFM F-3731,
<i>Bailiella aequalis</i> NFM F-3811.	
<i>Bailiella tenuicincta</i> NFM F-2972, NFM F-3168, NFM F-3169, NFM F-3200.	
<i>Clarella venusta</i> NFM F-3096, NFM F-3548, NFM F-3657.	
<i>Jincella applanata</i> NFM F-2794, NFM F-2820, NFM F-2825, NFM F-2831, NFM F-2832, NFM F-2934, NFM F-2949, NFM F-2964, NFM F-2965, NFM F-2975, NFM F-2976, NFM F-2977, NFM F-2978, NFM F-2979, NFM F-2993, NFM F-2994, NFM F-2995, NFM F-2996, NFM F-2997, NFM F-2998, NFM F-2999, NFM F-3000, NFM F-3001, NFM F-3003, NFM F-3005, NFM F-3006, NFM F-3010, NFM F-3012, NFM F-3013, NFM F-3014, NFM F-3015, NFM F-3018, NFM F-3019, NFM F-3020, NFM F-3021, NFM F-3022, NFM F-3023, NFM F-3024, NFM F-3025, NFM F-3032, NFM F-3033, NFM F-3080, NFM F-3082, NFM F-3083, NFM F-3084, NFM F-3085, NFM F-3086, NFM F-3087, NFM F-3088, NFM F-3089, NFM F-3090, NFM F-3091, NFM F-3092, NFM F-3093, NFM F-3094, NFM F-3103, NFM F-3104, NFM F-3105, NFM F-3106, NFM F-3107, NFM F-3110, NFM F-3111, NFM F-3112, NFM F-3113, NFM F-3114, NFM F-3115, NFM F-3116, NFM F-3117, NFM F-3118, NFM F-3119, NFM F-3120, NFM F-3121, NFM F-3122, NFM F-3123, NFM F-3124, NFM F-3125, NFM F-3126, NFM F-3127, NFM F-3128, NFM F-3129, NFM F-3130, NFM F-3131,	

Appendix 1. — Continuation.

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NFM F-3837, NFM F-3838, NFM F-3847, NFM F-3848,
NFM F-3896, NFM F-3897, NFM F-3899, NFM F-3900,
NFM F-3901, NFM F-3914, NFM F-3942, NFM F-3943,
NFM F-3944.

Meneviella venulosa NFM F-3178,
NFM F-3210, NFM F-3213, NFM F-3214, NFM F-3419,
NFM F-3600, NFM F-3601, NFM F-3602, NFM F-3603,
NFM F-3604, NFM F-3655, NFM F-3656, NFM F-3736,
NFM F-3737, NFM F-3738, NFM F-3930.

Paradoxides davidis NFM F-2814, NFM F-2815,
NFM F-2817, NFM F-2818, NFM F-2823, NFM F-2824,
NFM F-2826, NFM F-2827, NFM F-2980, NFM F-2981,
NFM F-2982, NFM F-3011, NFM F-3081, NFM F-3095,
NFM F-3097, NFM F-3098, NFM F-3099, NFM F-3100,
NFM F-3101, NFM F-3102, NFM F-3156, NFM F-3171,
NFM F-3172, NFM F-3173, NFM F-3174, NFM F-3175,
NFM F-3179, NFM F-3191, NFM F-3374, NFM F-3377,
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NFM F-3842, NFM F-3902, NFM F-3903, NFM F-3904,
NFM F-3905, NFM F-3906, NFM F-3907, NFM F-3908,
NFM F-3909, NFM F-3910, NFM F-3911, NFM F-3912,

NFM F-3913, NFM F-3916, NFM F-3917, NFM F-3918,
NFM F-3919, NFM F-3920, NFM F-3921, NFM F-3922,
NFM F-3923, NFM F-3924, NFM F-3925, NFM F-3926,
NFM F-3927, NFM F-3928, NFM F-3931, NFM F-3932,
NFM F-3933, NFM F-3936, NFM F-3937, NFM F-3938,
NFM F-3939, NFM F-3940, NFM F-3941.

Plutonides hicksii NFM F-2778, NFM F-2781,
NFM F-2782, NFM F-2783, NFM F-2784, NFM F-2789,
NFM F-2792, NFM F-2793, NFM F-2795, NFM F-2796,
NFM F-2805, NFM F-2806, NFM F-2813, NFM F-2816,
NFM F-2819, NFM F-2821, NFM F-2822, NFM F-2828,
NFM F-2829, NFM F-2830, NFM F-2833, NFM F-2861,
NFM F-2878, NFM F-2930, NFM F-2970, NFM F-2971,
NFM F-3002, NFM F-3004, NFM F-3008, NFM F-3009,
NFM F-3016, NFM F-3017, NFM F-3026, NFM F-3027,
NFM F-3028, NFM F-3030, NFM F-3031, NFM F-3036,
NFM F-3067, NFM F-3075, NFM F-3176, NFM F-3177,
NFM F-3193, NFM F-3194, NFM F-3208, NFM F-3209,
NFM F-3220, NFM F-3227, NFM F-3228, NFM F-3230,
NFM F-3231, NFM F-3232, NFM F-3236, NFM F-3241,
NFM F-3243, NFM F-3244, NFM F-3246, NFM F-3247,
NFM F-3248, NFM F-3249, NFM F-3252, NFM F-3253,
NFM F-3258, NFM F-3259, NFM F-3272, NFM F-3282,
NFM F-3283, NFM F-3286, NFM F-3292, NFM F-3299,
NFM F-3300, NFM F-3301, NFM F-3302, NFM F-3303,
NFM F-3304, NFM F-3308, NFM F-3309, NFM F-3320,
NFM F-3340, NFM F-3347, NFM F-3350, NFM F-3352,
NFM F-3353, NFM F-3354, NFM F-3360, NFM F-3361,
NFM F-3367, NFM F-3368, NFM F-3370, NFM F-3382,
NFM F-3433, NFM F-3444, NFM F-3445, NFM F-3450,
NFM F-3452, NFM F-3460, NFM F-3461, NFM F-3462,
NFM F-3475, NFM F-3716, NFM F-3717, NFM F-3744,
NFM F-3781, NFM F-3808, NFM F-3821, NFM F-3824,
NFM F-3834, NFM F-3836, NFM F-3849, NFM F-3882,
NFM F-3884, NFM F-3894, NFM F-3898, NFM F-3945,
NFM F-3947, NFM F-3948, NFM F-3949, NFM F-3950.

Sao hirsuta NFM F-3420.