Fauna of the Sæterdal Formation (Cambrian Series 2, Stage 4) of North Greenland (Laurentia)

JOHN S. PEEL

Geological Society of Denmark
https://2dgf.dk

Received 13 December 2024
Accepted in revised form
17 January 2025
Published online
04 February 2025

Peel, J.S. 2025. Fauna of the Sæterdal Formation (Cambrian Series 2, Stage 4) of North Greenland (Laurentia). Bulletin of the Geological Society of Denmark, Vol. 74, pp. 1–13. ISSN 2245-7070. https://doi.org/10.37570/bgsd-2025-74-01

The fauna preserved in decalcified sandstones of the Sæterdal Formation (Cambrian Stage 4) of southern Peary Land, North Greenland (Laurentia) is dominated by the trilobites *Kootenia marcoui* and *Bonnia brennus*, which also occur in the equivalent dark carbonates and mudstones of the Henson Gletscher Formation to the west. They are associated with *Olenellus* and small ptychoparioid trilobites. Brachiopods compared to *Nisusia ancauchensis*, originally described from the Precordillera terrane in Argentina, show variation in shell morphology and the form of the pseudodeltidium. They occur together with *Kutorgina* cf. *cingulata*, which is conspicuous in the overlying Paralledal Formation, rare *Matutella* sp. and an indeterminate hyolithid.

Keywords: Trilobites, brachiopods, Cambrian Stage 4, North Greenland, Laurentia.

John S. Peel, [john.peel@pal.uu.se], Department of Earth Sciences (Palaeobiology), Uppsala University, Villavägen 16, SE–75236 Uppsala, Sweden.

The Sæterdal Formation (Cambrian Series 2, Stage 4) of Peary Land, North Greenland, crops out in a narrow belt along the northern side of Wandel Dal from 'Midsommersøer' via Sæterdal to Parallelдal in the east (Fig. 1C; Ineson & Peel 1997). In the type area of Sæterdal the formation consists of about 130 m of recessive pale buff sandstones (Fig. 1A) lying between pale dolostones of the Aftenstjernesø and Paralleldal formations in steep cliffs above the dark, recessive mudstones and sandstones of the Buen Formation (Cambrian Stages 3–4), heralding the establishment of the Cambrian–Silurian carbonate platform that dominates southern Peary Land and much of northern Greenland to the west (Higgins et al. 1991a, b). The Wandel Dal outcrops of the formation are sub-parallel to strike but the pale sandstones of the formation interdigitate with dark mudstones and carbonates of the Henson Gletscher Formation in the 'Midsommersøer'–Fimbuldal area, in which they form a prominent middle member (Fig. 1B), to the west. From a regional perspective, the Sæterdal Formation consists of a wedge of sandstones, probably transported seawards during severe storms and interrupting the deposition of the outer shelf–slope carbonates and mudstones that comprise the Henson Gletscher Formation (Higgins et al. 1991a, b). The Sæterdal Formation thins out 18 km to the east of the type section, where the Paralleldal Formation directly overlies the Aftenstjernesø Formation (Ineson & Peel 1997).

The Sæterdal Formation is poorly fossiliferous but trilobites (Fig. 2) and brachiopods (Figs 3–6) may be locally abundant in the Sæterdal area where the moulds of the decalcified fossils display a distinctive orange brown colouration. Trilobites, including *Olenellus* Hall, 1861, indicate an early Cambrian age (Cambrian Series 2, Stage 4), with *Bonnia brennus* (Walcott, 1916) and *Kootenia marcoui* (Whitfield, 1884) documented by Blaker & Peel (1997) also in the Henson Gletscher Formation in outcrops to the west. Oryctocephalid trilobites definitive of the latest Cambrian Stage 4, *Ovatoryctocara granulata* assemblage (Blaker & Peel 1997; Geyer & Peel 2011; Peel et al. 2016) are not recorded from the Sæterdal Formation, likely indicating that the latter formation is slightly older than the *Ovatoryctocara granulata* assemblage of the Henson Gletscher Formation. However, this assemblage occurs in dark carbonates and mudstones in the Henson Gletscher Formation quite unlike the sandstones of the Sæterdal Formation, suggesting that the difference may be related to sedimentary facies. Similarly, the brachiopod fauna of the Sæterdal Formation lacks the organophosphatic linguliformean brachiopods that dominate the *Ovatoryctocara granulata* assemblage of the Henson Gletscher Formation in western Peary Land (Peel et al. 2016).

The present paper revisits the fauna of the Sæterdal Formation, additionally describing brachiopods, mainly *Nisusia* Walcott, 1905 and *Kutorgina* Billings, 1861, and a rare hyolithid. *Kutorgina* is abundant in the Paralleldal Formation some 20 km to the east (Popov et al. 1997) but was also described from the Bastion Formation of North-East Greenland by Poulsen (1932) and Skovsted & Holmer (2005) and from the Wulff River Formation of Inglefield Land, North-West Greenland (Poulsen 1958). The fauna as a whole is similar in general composition and preservation to that of the lower Cambrian lower Parker Shale of Vermont documented by Shaw (1954, 1955).

Of particular interest is the occurrence in the Sæter-

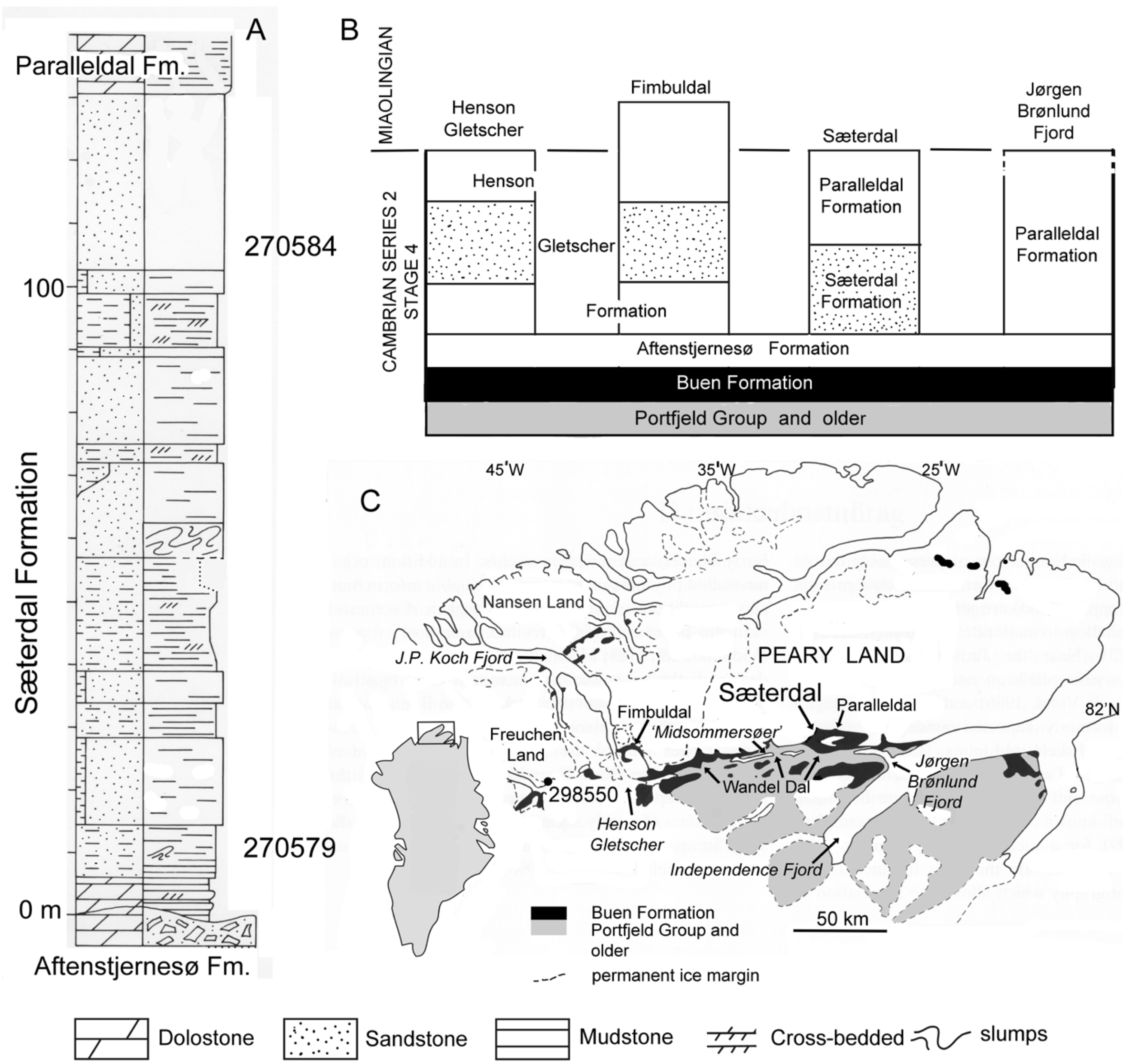

Fig. 1. A: type section of the Sæterdal Formation measured by J.R. Ineson in 1979 (Ineson & Peel 1997, fig. 69) showing the equivalent location of *in situ* faunas (GGU numbers) collected during 1978, about 2 km to the south-west of the type section, and described herein. **B**: distribution of sandstone-dominated intervals (stippled) in the Sæterdal and Henson Gletscher formations of southern Peary Land. C, locality map with a regional datum provided by the dark siliciclastic sediments of the Buen Formation (black). Carbonate rich sediments and pale sandstones of Cambrian Series 2, Stage 4 (see B) form a narrow outcrop immediately to the north of the outcrop belt of the Buen Formation. 'Midsommersøer' consists of Øvre Midsommersø in the west and Nedre Midsommersø in the east. Derivation of GGU sample 298550 from the Henson Gletscher Formation in southern Freuchen Land.

dal Formation of *Nisusia* cf. *ancauchensis* (Figs 3, 4), a species originally described by Benedetto & Foglia (2012) from the uppermost beds of the Ancaucha olistolith near Jáchal City, San Juan province, Argentina (Cambrian Stage 4). Assignment of the North Greenland material to *Nisusia* cf. *ancauchensis* supports the recognition of the Precordillera terrane of Argentina as a microcontinent derived from Laurentia (Keller et al. 1998; Bordonaro et al. 2013; Pratt & Bordonaro 2014). A single specimen of *Nisusia* from the uppermost Henson Gletscher Formation (Cambrian Stage 4, *Ovatoryctocara granulata* assemblage) of southern Freuchen Land is included for comparative purposes.

Material

All material from the Sæterdal Formation was collected on the north-western side of Sæterdal, Peary Land, North Greenland (82°17′09′′N, 32°45′W). The locality is situated about 2 km south-west of the type section of the formation (Ineson & Peel 1997, fig. 68A).

GGU samples 270579 and 270584 were collected by J.S. Peel on 4th August 1978 at about 10 m above the base (GGU sample 270579) and about 25 m below the top (GGU sample 270584) of the formation (Fig. 1A). Other GGU samples 270563–270590 were collected by J.S. Peel on 3rd–5th August 1978. Each of these samples is derived from an individual talus block from the outcrop of the formation at an altitude of about 425 m a.s.l.

GGU sample 298550 was collected by J.S. Peel on 15th July 1985 from the uppermost Henson Gletscher Formation in southern Freuchen Land (82°09´N, 42°25´W), about 45 km west of Henson Gletscher (Geyer & Peel 2011, fig. 1D, locality 1; see also Streng et al. 2016; Oh et al. 2024).

Following mechanical preparation, specimens from the Sæterdal Formation were coated with colloidal carbon black in aqueous suspension, dried and then whitened prior to photography with ammonium chloride sublimate from a hot glass tube. The specimen from GGU sample 298550 is silicified and was extracted from the host limestone with weak acetic acid prior to scanning electron microscopy. All images were assembled in Adobe Photoshop 7 and CS4.

Systematic palaeontology

Repositories and abbreviations. GGU prefix indicates a sample made as a participant in the North Greenland Project (1978–1985), a regional mapping programme of Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), now the Geological Survey of Denmark and Greenland, Copenhagen, Denmark (GEUS). Type and figured specimens are deposited in the type collection of the Natural History Museum of Denmark, Copenhagen (MGUH prefix) and the Museum of Evolution, Uppsala University (PMU prefix).

Phylum Arthropoda Siebold, 1848

Class Trilobita Walch, 1771

Order Redlichida Richter, 1932

Suborder Olenellina Walcott, 1890

Superfamily Olenelloidea Walcott, 1890

Family Olenellidae Walcott, 1890

Genus *Olenellus* Hall, 1861

Type species. *Olenus thompsoni* Hall, 1859 from the lower Cambrian of Vermont, U.S.A.

***Olenellus* cf. *howelli* Meek *in* White, 1874**
Fig. 2G, I

1997 *Olenellus* cf. *O. gilberti*; Blaker & Peel, p. 60, fig. 55.10, 55.12, 55.13.

Figured material. Cephala; MGUH 23229 from GGU sample 270584 and MGUH 34845 from GGU sample 270563, Sæterdal Formation, Cambrian Series 2, Stage 4.

Other material. GGU samples 270565, 270568, 270582, 270584, 270587, 270589, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. Olenellid cephala from the Sæterdal Formation are indifferently preserved due to their occurrence in coarse sandstone; other skeletal elements are not known. Blaker & Peel (1997) compared this species to *Olenellus gilberti* Meek *in* White, 1874, which was described with a detailed morphological analysis by Webster (2015), following earlier descriptions by Palmer (1957, 1998).

Specimens of *Olenellus gilberti* illustrated by Webster (2015) display a well-marked anterior deflection of the border between the intergenal angle and the genal angle whereas the posterior border continues as a uniform curve out to the genal angles in the Sæterdal material (Fig. 2G). In this feature it more closely resembles *Olenellus howelli* (Meek *in* White, 1874) and *Olenellus fowleri* Palmer, 1998 as illustrated by Palmer (1998, fig. 9.5) from the Pioche Formation of Nevada. However, the palpebral lobes of *Olenellus howelli* differ in extending to the posterior furrow, while *Olenellus fowleri* has a well developed plectrum joining the glabella to the anterior border. Genal spines in the Sæterdal material are slender and about 40% of the length of the cranidium, although not preserved in either of the illustrated specimens.

Order Corynexochida Kobayashi, 1935

Family Dorypygidae Kobayashi, 1935

Genus *Bonnia* Walcott, 1916

Type species. *Bathyurus parvulus* Billings, 1861 from the lower Cambrian of Labrador.

***Bonnia brennus* (Walcott, 1916)**
Figs 2C, J, L–O, R

1916 *Corynexochus brennus* Walcott, p. 314, pl. 57, figs 3–3b.
1948 *Bonnia brennus*; Rasetti, p. 16, pl. 3, figs 16–25 (includes synonomy).
1997 *Bonnia brennus*; Blaker & Peel, p. 87, figs 50, 51.1–5, 51.8, 51.10.
2016 *Bonnia* cf. *brennus*; Peel et al., figs 3U, V, 4G, N.

Figured material. Cranidia: MGUH 23361 and MGUH 23362 from GGU sample 270563. Pygidia: MGUH 23368 from GGU sample 270579, MGUH 34843 from GGU sample 270563. Hypostome: MGUH 34842 from GGU sample 270563, Sæterdal Formation, Cambrian Series 2, Stage 4.

Other material. GGU samples 270565 and 270587, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. A full description of *Bonnia brennus* was given by Blaker & Peel (1997) on the basis of material from the Henson Gletscher and Sæterdal formations in North Greenland. Disarticulated cranidia and pygidia are common in the Sæterdal Formation. A single hypostome (Fig. 2C) is proportionately slightly wider than specimens illustrated by Blaker & Peel (1997, figs 50.7, 50.8, 50.12) and Peel et al. (2016, fig. 4N) from the Henson Gletscher Formation. It is distinguished from hypostomes of the co-occurring *Kootenia marcoui* (Whitfield, 1884) by its angular anterior margin and well developed antero-lateral wings.

Genus *Kootenia* Walcott, 1889

Type species. Baythyuriscus (Kootenia) dawsoni Walcott, 1889 from the middle Cambrian (Miaolingian Series) of British Columbia, Canada.

***Kootenia marcoui* (Whitfield, 1884)**
Fig. 2E, F, H, K

1884 *Dikellocephalus*? *marcoui* Whitfield, p. 150, pl. 14, fig. 7.
1997 *Kootenia marcoui*; Blaker & Peel, p. 90–95, figs 52, 53, 54.1–6, 54.10, 54.11 (includes synonomy).

Figured material. Cranidium: MGUH 23378 from GGU collection 270590. Pygidia: MGUH 23399 from GGU collection 270590 and MGUH 23401 from GGU collection 270564, Sæterdal Formation, Cambrian Series 2, Stage 4.

Other material. Abundant in most samples from the Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. Kootenia marcoui is distinguished from other lower Cambrian species of the genus in North Greenland by its seven pairs of pygidial spines (Blaker & Peel 1997). Disarticulated cranidia and pygidia of *Kootenia marcoui* are common in the samples from the Henson Gletscher Formation in western Peary Land and in the Sæterdal Formation.

Family Zacanthoididae Swinnerton, 1915

Genus *Zacanthopsis* Resser, 1938

Type species. Olenoides levis Walcott, 1886 from the lower Cambrian of Pioche, Nevada, U.S.A.

***Zacanthopsis* sp.**
Fig. 2D

Figured material. MGUH 34844 from GGU sample 270587, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. Within the limits imposed by its poor preservation, this single internal mould of a cranidium can be compared with *Zacanthopsis blakeri* Geyer & Peel, 2011 from the Henson Gletscher Formation of western Peary Land, originally referred to *Zacanthopsis levi* (Walcott, 1886) by Blaker & Peel (1997). Unfortunately, most of the broad convex anterior border has been worn away.

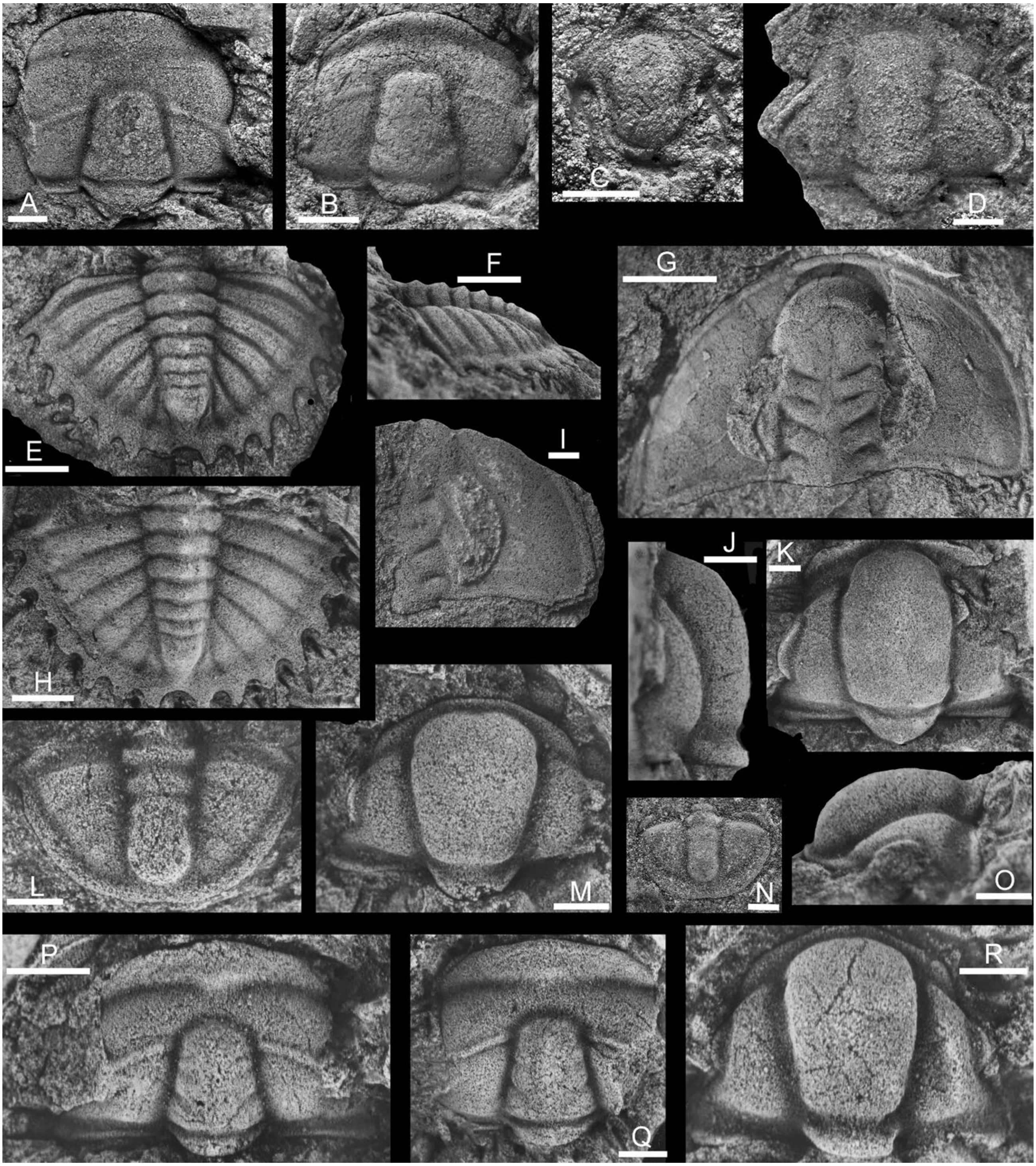

Fig. 2. Trilobites from the Sæterdal Formation (Cambrian Stage 4), Sæterdal, North Greenland; internal moulds. **A:** Undetermined ptychopariid, MGUH 34840 from GGU sample 270563, cranidium. **B:** *Anebocephalus*? sp., MGUH 34841 from GGU sample 270563, cranidium. **C, J, L–O, R:** *Bonnia brennus* (Walcott, 1916). **C:** MGUH 34842 from GGU sample 270563, hypostome. **J, R:** MGUH 23362 from GGU sample 270563, cranidium in lateral (J) and dorsal (R) views. **L:** MGUH 23368 from GGU sample 270579, pygidium. **M, O:** MGUH 23361 from GGU sample 270563, cranidium in dorsal (M) and lateral (O) views. **N:** MGUH 34843 from GGU sample 270563 pygidium. **D:** *Zacanthopsis* sp., MGUH 34844 from GGU sample 270587, cranidium with broken anterior. **E, F, K, H:** *Kootenia marcoui* (Whitfield, 1884).**E, F:** MGUH 23401 from GGU sample 270564, pygidium in dorsal (E) and lateral (F) views. **K:** MGUH 23378 from GGU sample 270564, cranidium. **H:** MGUH 23399 from GGU sample 270590, pygidium. **G, I:** *Olenellus* cf. *howelli* Meek *in* White, 1874. **G:** MGUH 23229 from GGU sample 270584, cranidium. **I:** MGUH 34845 from GGU sample 270563, broken cranidium. **P, Q:** *Harklessaspis*? sp. **P:** MGUH 23581 from GGU sample 270568, cranidium. **Q:** MGUH 23582 from GGU sample 270563, cranidium. Scale bars: 1 mm (J); 2 mm (A–D, G, I, K–O, Q, R); 3 mm (H); 4 mm (E, F, P)

Order Ptychopariida Swinnerton, 1915

Remarks. In available material, small ptychopariidans are known only from isolated cephala, with the result that generic assignments are tenuous.

Genus *Anebocephalus* Sundberg & Webster, 2022

Type species. *Anebocephalus silverpeakensis* Sundberg & Webster, 2022 from the Harkless Formation, Cambrian Series 2, (mid-Dyeran Regional Stage), Nevada, U.S.A.

***Anebocephalus*? sp.**
Fig. 2B

Figured material. MGUH 34841 from GGU sample 270563, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. The anterior margin of this internal mould of a cranidium (Fig. 2B) is more convexly curved in dorsal view than in *Eoptychoparia pearylandica* Geyer & Peel, 2011 from the Henson Gletscher Formation (Cambrian Stage 4), but the specimens illustrated by Geyer & Peel (2011, fig. 21) show variation both in the curvature and the width of the brim. The posterolateral extensions of the fixigenae are not exposed. The transverse width of the fixigenae at the anterior margin of the eye is slightly greater than the corresponding width of the glabella. *Eoptychoparia pearylandica* was referred to *Anebocephalus* by Sundberg & Webster (2022).

Cranidia of *Onchocephalus*? *freucheni* Geyer & Peel, 2011, also from the Henson Gletscher Formation (Cambrian Stage 4), differ in terms of a more parallel-sided glabella and a straight anterior border furrow. *Onchocephalus*? *freucheni* was referred to the new genus *Coenoides* by Sundberg & Webster (2022), with type species *Coenoides scholteni* Sundberg & Webster (2022) from the upper Harkless Formation, Nevada.

Genus *Harklessaspis* Sundberg & Webster, 2022

Type species. *Harklessaspis parvigranulosus* Sundberg & Webster, 2022, from the Harkless Formation, Cambrian Series 2 (Dyeran Regional Stage), Nevada, U.S.A.

***Harklessaspis*? sp.**
Fig. 2P, Q

1997 Ptychoparioid genus and species undetermined B, Blaker & Peel, p. 132, fig. 51.6?, 51.9, 51.11.
1997 Ptychoparioid genus and species undetermined C, Blaker & Peel, p.133, fig. 51.7.

Figured material. Cranidia; MGUH 23581 from GGU sample 270568; MGUH 23582 from GGU collection 270563. Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. Blaker & Peel (1997) placed the two illustrated specimens (Fig. 2P, Q) in separate species, but they are united here, given their relatively poor preservation and the variation in the shape of the front border illustrated by Sundberg & Webster (2022) in the type species. The degree of expression of the median expansion within the anterior border varies, but the border furrow itself is characteristically deep to either side.

Undetermined ptychopariid
Fig. 2A

Figured material. Cranidium: MGUH 34840 from GGU sample 270563, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. The glabella of this internal mould is proportionately shorter than in *Harklessaspis*? sp., while the brim is wider anteriorly and less sharply defined.

Phylum Brachiopoda Duméril, 1806

Subphylum Rhynchonelliformea Williams *et al*., 1996

Class Kutorginata Williams *et al*., 1996

Order Kutorginida Kuhn, 1949

Superfamily Nisusioidea Walcott & Schuchert *in* Walcott, 1908

Family Nisusiidae Walcott & Schuchert *in* Walcott, 1908

Genus *Nisusia* Walcott, 1905

Type species. *Orthisina festinata* Billings, 1861, Potsdam Group, Cambrian Series 2; Vermont, U.S.A.

Remarks. Bell (1941) divided nisusiids into two groups on the basis of their shape and the location of the ventral umbo. Mao et al. (2017) listed 39 species of *Nisusia* from the Cambrian but Holmer et al. (2019) considered only half of these in their cladistic analysis. Holmer et al. (2019) recognised two clades of nisusiids, with most species referred to a group in which the umbo is elevated above the rest of the ventral valve (cf. Figs 3I, 4D), which is shallowly concave behind the umbo in lateral profile. The second group included mainly non-spinose species with biconvex shells. They suggested that Laurentia was the main place for nisusiid dispersal during Cambrian Series 2 with possible records existing from Cambrian Stage 3 (Saxen 2017), although *Nisusia alaica* (Popov & Tikhonov, 1990) was described from Cambrian Stage 3 in the Kyrgyz Republic. Cambrian Stage 4 representatives include the type species *Nisusia festinata* (Billings, 1861), originally described from Vermont (Billings 1861, p. 10, figs 11, 12), and *Nisusia ancauchensis* Benedetto & Foglia, 2012, described from the Precordillera terrane in Argentina (Benedetto & Foglia 2012, fig. 4.1–4.5).

Oh et al. (2022) analysed the phylogeny and distribution of *Nisusia*, adding a few more species to the data base of Holmer et al. (2019) and recognising two clades descended from a paraphyletic basal group. Spinose taxa occur in all three groups. *Nisusia festinata* and *Nisusia ancauchensis* were placed in separate clades and considered to be derived from a basal group with strong and long spines. Such coarse spines are known in *Nisusia alaica* and *Nisusia metula* Brock et al., 1998, the latter from Cambrian Series 3 (Miaolingian) in New South Wales. A silicified juvenile specimen referred to *Nisusia* sp. undet. from the uppermost Henson Gletscher Formation (Cambrian Series 2, Stage 4, *Ovatoryctocara* assemblage; Fig. 4K–N) in southern Freuchen Land, about 45 km west of Henson Gletscher, also displays coarse spines that are much more prominent than those preserved in specimens of *Nisusia* from the Sæterdal Formation (Figs 3A–Q, 4A–J).

***Nisusia* cf. *ancauchensis* Benedetto & Foglia, 2012**
Figs 3A–I, K–Q, 4A–J

Figured material. MGUH 34846, MGUH 34848–34853, MGUH 34857 and MGUH 34858 from GGU sample 270563; MGUH 34847 and MGUH 34856 from GGU 270587; MGUH 34855 from GGU sample 270566. Sæterdal Formation, Cambrian Series 3, Stage 4.

Description. All specimens from the Sæterdal Formation occur in decalcified sandstone as external moulds (Fig. 3N, O) and composite moulds with variable preservation of the strongly costellate outer surface and growth lines. Herein, the relief of described morphological features relates to their form on the specimens as illustrated. Conjoined valves have not been observed. Maximum observed width is about 15 mm, length 11 mm, measured on a ventral valve. Greatest width is slightly anterior of the hinge line.

The highest point of the ventral valve lies at the pointed umbo, which may extend posteriorly to overhang the apsacline to catacline interarea (Figs 3K, L, 4C–D) or rise abruptly from the valve surface (Fig. 3I, P). The foramen is apparently located at the apex of the umbo (Fig. 4B, C, E). In lateral profile the ventral valve is initially flattened, sometimes shallowly concave (Figs 3H, 4H) behind the umbo before increasing in convexity towards the anterior margin (Figs 3C, 4D). The ventral surface may show a median sinus posteriorly (Fig. 4E) but its anterior margin is almost planar (Fig. 3D) or even with a shallow fold (Fig. 3P). The junction between the ventral surface and interarea is angular, usually with a prominent rounded cord along the crest (Figs 3B, G, M, 4E, J). The pseudodeltidium varies from transversely narrow (Fig. 3B) with grooved margins near the apex (Figs 3G, 4I) to wide with diffuse margins (Fig. 4B, C); it may be depressed medially (Fig. 3B) or uniformly convex (Fig. 3G, H). The depth of the open delthyrium is about half the height of the interarea (Fig. 3M, arrow). Grooves delimiting the margins of the adapical portion of the pseudodeltidium may curve onto the valve surface (Figs 3G, 4I). In one specimen (Fig. 3F) the grooves persist almost to half the length, suggesting an association with muscle scars. Radial dorsal ornamentation initially consists of 7–10 costellae close to the umbo, with only two or three on the projecting apex (Fig. 3K, L). About 30 radial elements are present at the anterior margin due to progressive interdigitation of additional costellae (Fig. 3A). Comarginal ornamentation consists of obscure fine growth lines and more prominent cords. Tubercles (fine spine bases) occur at the intersection of the cords and costellae (arrows in Figs 3A, D, 4E) and are seen as pits in the external mould (arrows in Figs 3N, O).

The dorsal valve is poorly known, with a rounded apex. Its radial ornamentation is crossed by comarginal growth lines but may be subdued except near the anterior margin (Figs 3Q, 4F), as in one ventral valve (Fig. 3P). However, ornamentation is uniformly developed, with spines, in an external mould (arrow in Fig. 3O).

Remarks. Specimens from the Sæterdal material show variation in terms of shell shape and the nature of the pseudodeltidium. End members in this continuum (Figs 3A–D, 4A–E) could easily be assigned to different species, but on account of the small sample size, ontogenetic variation and the lack of information concerning the dorsal interarea, they are collectively compared to *Nisusia ancauchensis* Benedetto & Foglia, 2012, while recognising similarities with some of the varied material assigned by Walcott (1912) to the type species *Nisusia festinata*. However, unlike the Sæterdal specimens, some material from Vermont assigned to *Nisusia festinata* by Walcott (1912) and Shaw (1955) has the hinge line extended into alae and forming the greatest width of the shell.

Material assigned to *Nisusia ancauchensis* was based on a few specimens described by Benedetto & Foglia

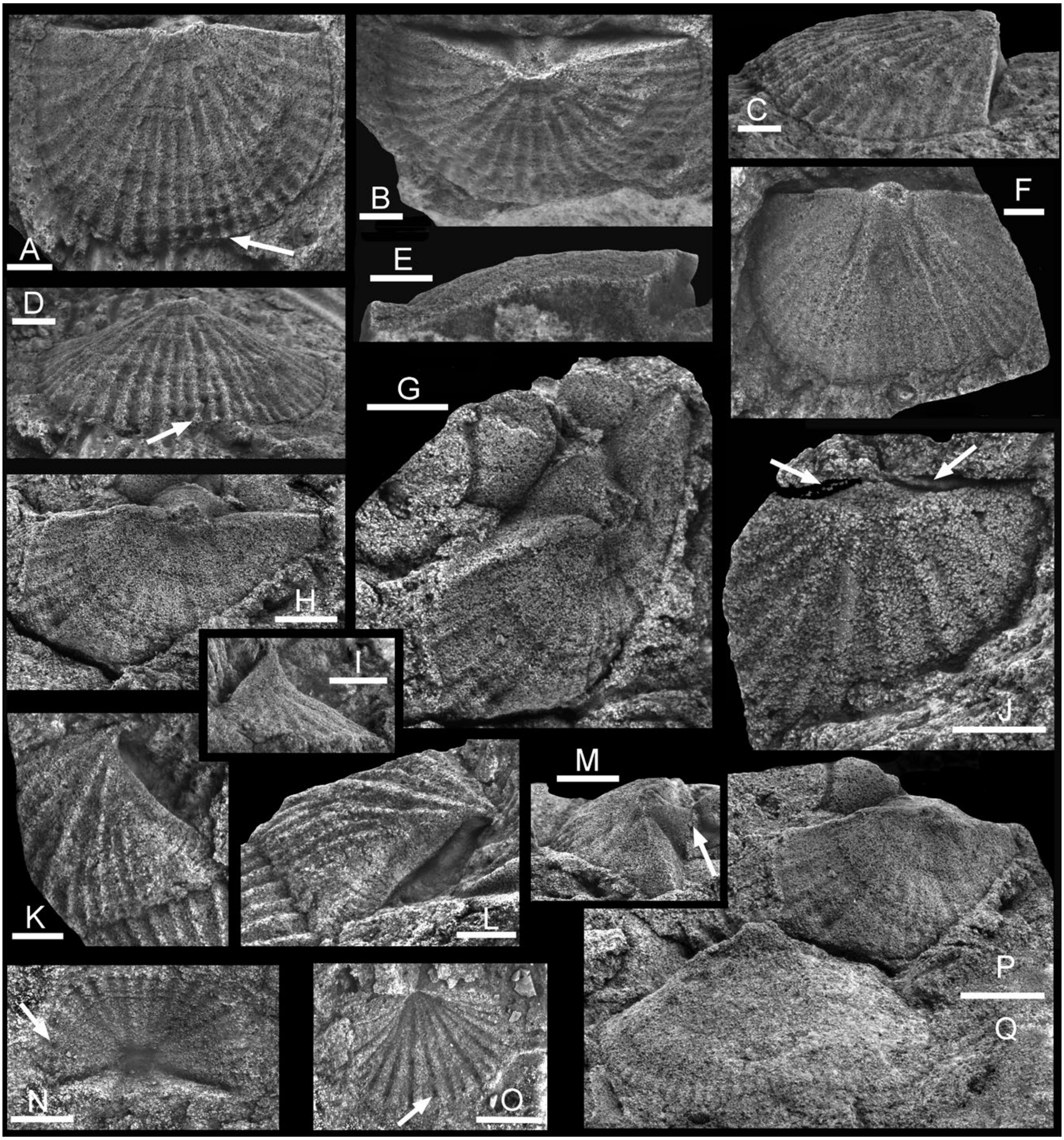

Fig. 3. Brachiopods from the Sæterdal Formation (Cambrian Stage 4), Sæterdal, North Greenland. **A–I, K–Q:** *Nisusia* cf. *ancauchensis* Benedetto & Foglia, 2012. **A–D:** MGUH 34846 from GGU sample 270563, ventral (A), postero-ventral (B), lateral (C) and oblique anterior (D) views of ventral valve, with arrows indicating spine bases. **E, F:** MGUH 34847 from GGU sample 270587, lateral (E) and ventral (F) views of ventral valve, with apex broken away. **G, H, M, P:** MGUH 34848 from GGU sample 270563, oblique postero-ventral (G), ventral (H, P) and postero-lateral (M) views of ventral valve with arrow in M indicating delthyrium. **I:** MGUH 34849 from GGU sample 270563, ventro-lateral view of ventral valve. **K, L:** MGUH 34850 from GGU sample 270563, oblique views of central valve. **N:** MGUH 34851 from GGU sample 270563, external mould of ventral valve with hole produced by spine (arrow). **O:** MGUH 34852 from GGU sample 270563, external mould of dorsal valve, with holes produced by spines (arrow). **Q:** MGUH 34853 from GGU sample 270563, antero-ventral view of ventral valve on same slab as P. **J:** *Nisusia* sp., MGUH 34854 from GGU 270563, dorsal view of dorsal valve with cardinal ridges arrowed. Scale bars: 2 mm (A–N); 3 mm (O, P).

(2012) from the uppermost beds of the Ancaucha olistolith at Quebrada Ancaucha, about 30 km west of Jáchal City, San Juan province, Argentina (Cambrian Stage 4). Benedetto & Foglia (2012) commented that the pseudodeltidium of *Nisusia ancauchensis* was greatly enlarged, twice as wide as long, and unbounded by lateral furrows. This is seen in a ventral valve from GGU sample 270566 where the dark pits in the posterior view relate to shadow under the apsacline interarea rather than to sockets (Fig. 4B, C). Other similar specimens from GGU sample 270587 (Fig. 4E, I) show that the adapical part of the pseudodeltidium is parallel-sided before expansion. In an additional specimen it is bounded by a groove that deepens adapically (Fig. 3G, H, M) and terminates at an open delthyrium (arrow in Fig. 3M), although this groove is much narrower than that seen in *Nisusia alaica* (Popov & Tikhonov (1990, pl. 3, figs 21a, 23). More frequently, the pseudodeltidium expands slowly and uniformly, occupying about a quarter to a fifth of the width of the interarea (Fig. 3B) in a manner reminiscent of *Nisusia festinata* as illustrated by Billings (1861) and Walcott (1912).

A prominent, cord-like elevation along the angulation between the interarea and the valve surface in the holotype ventral valve of *Nisusia ancauchensis* (Benedetto & Foglia, 2012, fig. 4.1–4.4) is also seen specimens from Sæterdal (Figs 3B, G, 4E, I) but it is lacking in *Nisusia festinata*.

Apart from its longer and coarser spines, the silicified specimen of *Nisusia* sp. undet. from the Henson Gletscher Formation in southern Freuchen Land (Fig. 4K–N), displays a pseudodeltidium that is similar to some specimens of *Nisusia* cf. *ancauchensis* from the Sæterdal Formation (Figs 3G, 4E).

***Nisusia* sp.**
Fig. 3J

Figured material. MGUH 34854 from GGU sample 270563, Sæterdal Formation.

Remarks. A single internal mould of a shallowly convex dorsal valve attributed to *Nisusia* preserves about 15 coarse costellae with rare branching that in their coarseness resemble *Eoconcha* Cooper, 1951. Traces of ridges

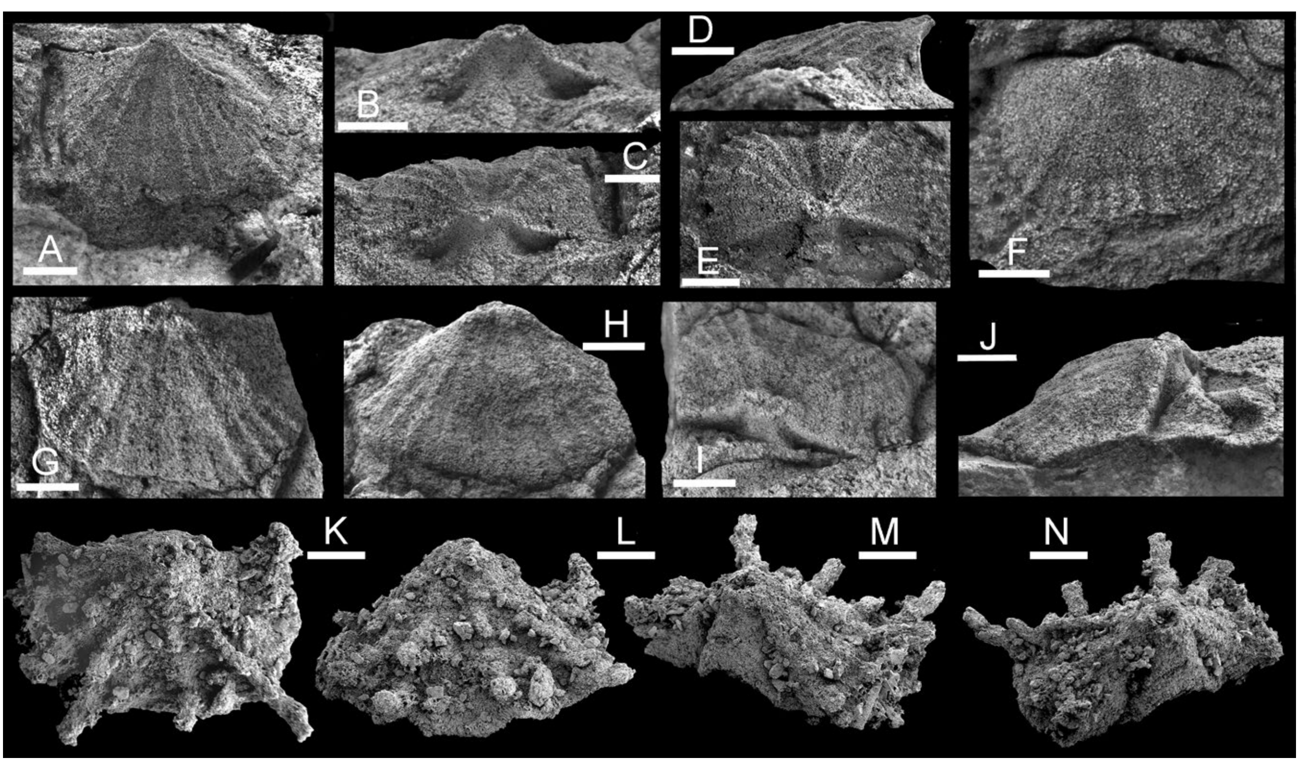

Fig. 4. *Nisusia* Walcott, 1905, Cambrian Stage 4, North Greenland. **A–J:** *Nisusia* cf. *ancauchensis* Benedetto & Foglia, 2012 from the Sæterdal Formation (Cambrian Stage 4), Sæterdal. **A–D:** MGUH 34855 from GGU sample 270566, ventral valve in ventral (A), postero-ventral (B, C) and lateral (D) views. **E:** MGUH 34856 from GGU sample 270587, ventral valve in postero-ventral view. **F:** MGUH 34857 from GGU sample 270563, dorsal valve. **G–J:** MGUH 34858 from GGU sample 270563, ventral valve in ventral (G), antero-ventral (H), postero-ventral (I) and postero-lateral (J) views. **K–N:** *Nisusia* sp. undet., uppermost Henson Gletscher Formation (Cambrian Stage 4), southern Freuchen Land. PMU 38495 from GGU sample 298550, silicified ventral valve in ventral (K), anterior (L) and posterior (M, N) views. Scale bars: 1 mm (K–N); 2 mm (A–J).

corresponding to linear cardinal sockets (Popov & Tikhonov 1990, fig. 3b) extend laterally from the apical area (Fig. 3O, arrows), which is slightly depressed as a result of thickening by a notothyrial plate on the shell interior.

Superfamily Kutorginoidea Schuchert, 1893

Family Kutorginidae Schuchert, 1893

Genus *Kutorgina* Billings, 1861

Type species. Kutorgina cingulata Billings, 1861, Cambrian Series 2, L'Anse au Loup (Belle Isle), Labrador, Canada.

***Kutorgina* cf. *cingulata* Billings, 1861**
Fig. 5A–C, F–I

Figured material. MGUH 34860–MGUH 34862 and MGUH 34864 from GGU sample 270563; MGUH 34863 from GGU sample 270566; MGUH 34859 from GGU sample 270587. Sæterdal Formation, Cambrian Series 3, Stage 4.

Remarks. Specimens of *Kutorgina* cf. *cingulata* Billings, 1861 from the Sæterdal Formation contrast markedly in terms of preservation with the silicified material described from the Paralleldal Formation by Popov et al. (1997). While the pronounced comarginal rugae are conspicuous in external and composite moulds (Fig. 5A–C), they are only weakly visible on internal moulds (Fig. 5F, G). Similar preservation was illustrated by Shaw (1955) in specimens from the lower Parker Shale of Vermont.

Order Chileata Williams *et al*., 1996

Superfamily Matutelloidea Andreeva, 1962

Family Matutellidae Andreeva, 1962

Genus *Matutella* Cooper, 1951

Type species. Matutella clarkei Cooper, 1951 from the Shady Formation, Cambrian Series 2, Austinville, Virginia, U.S.A.

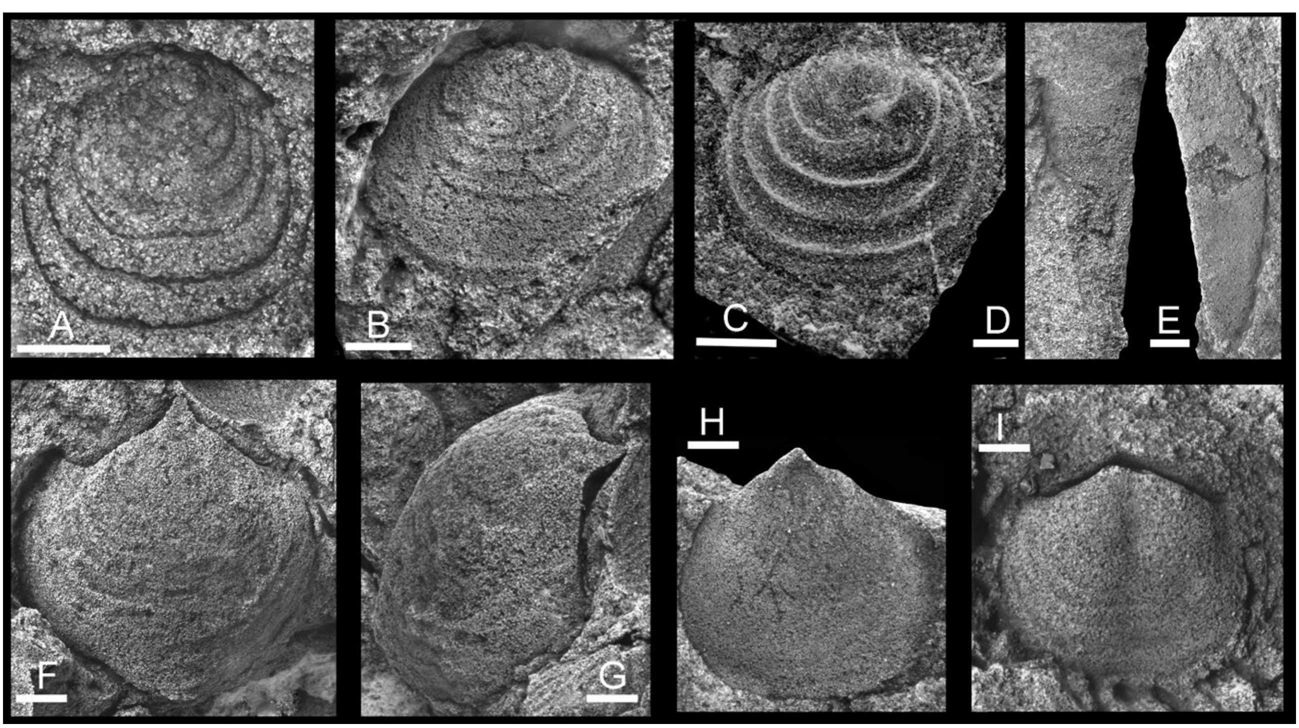

Fig. 5. *Kutorgina* cf. *cingulata* (Billings, 1861) and hyolithid from the Sæterdal Formation (Cambrian Stage 4), Sæterdal, North Greenland. GGU sample 270563 unless stated. **A–C, F–I:** *Kutorgina* cf. *cingulata* (Billings, 1861). **A:** MGUH 34859 from GGU sample 270587, composite mould of juvenile dorsal valve. **B:** MGUH 34860, composite mould of juvenile dorsal valve. **C:** MGUH 34861, digitally reversed external mould of juvenile dorsal valve. **F, G:** MGUH 34862, internal mould of ventral valve. **H:** MGUH 34863 from GGU sample 270566, internal mould. **I:** MGUH 34864, internal mould of dorsal valve. **D, E:** Hyolithid sp. indet. MGUH 34865 from GGU sample 270566, internal mould in dorsal (D) and lateral (E) views. Scale bars: 2 mm.

***Matutella* sp.**
Fig. 6

Figured material. MGUH 34866 from GGU sample 270563, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. This is known from a single, poorly preserved, incomplete internal mould of a dorsal valve. Traces of coarse costellae are retained lateral to the prominent dorsal fold. Preservation is too poor to permit meaningful comparison with material described by Cooper (1951), Andreeva (1962) and Aksarina & Pelman (1975).

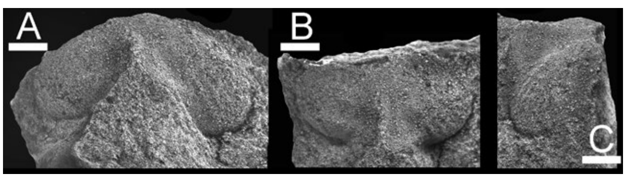

Fig. 6. *Matutella* sp., MGUH 34866 from GGU sample 270563, internal mould of dorsal valve in oblique anterior (A), dorsal (B) and lateral (C) views. Sæterdal Formation, Cambrian Series 2, Stage 4. Scale bars: 3 mm.

Phylum uncertain

Class Hyolitha Marek, 1963

Order Hyolithida Syssoiev, 1957

Hyolithid sp. indet.
Fig. 5D, E

Figured material. MGUH 34865 from GGU sample 270566, Sæterdal Formation, Cambrian Series 2, Stage 4.

Remarks. A single, poorly preserved conch has a transversely uniformly convex dorsum and rounded angular transitions to the flattened basal surface. The conch is curved slightly towards the dorsum; the presence of a ligula is not confirmed.

Acknowledgements

Yeungju Oh (Korea Polar Research Institute and University of Science and Technology, Daejeon) and Michael Streng (Uppsala) are thanked for discussions concerning *Nisusia*. Jon R. Ineson (GEUS) is thanked for permission to reproduce the geological column (Fig. 1A). Jan Ove R. Ebbestad (Uppsala) and Tim Topper (Stockholm) are acknowledged for reviews of the manuscript.

References

Aksarina, N.A. & Pelman, Yu.L. 1978: Cambrian brachiopods and bivalved molluscs of Siberia. Akademiya Nauk SSSR, Institut geologii i geofiziki, Sibirskoe otdeleniie 362, 5–178. [in Russian]

Andreeva, O.N. 1962: Nekotorye kembriyskie brakhiopody Sibiri i Sredney Asii [Some Cambrian brachiopods of Siberia and Central Asia]. Paleontologicheskiy Zhurnal 1962(2), 87–96.

Bell, W.C. 1941: Cambrian Brachiopoda from Montana. Journal of Paleontology 15, 193–255.

Benedetto, J.L. & Foglia, R.D. 2012: Lower and Middle Cambrian rhynchonelliform brachiopods from the Precordillera Terrane of Argentina. Journal of Paleontology 86, 273–281. https://doi.org/10.1666/10-115.1

Billings, E. 1861: On some new or little known species of Lower Silurian fossils from the Potsdam Group (Primordial Zone). In: Hitchcock, E., Hitchcock, E., Jr, Hager, A.D. & Hitchcock, C.H., Report on the Geology of Vermont: descriptive, theoretical, economical, and scenographical 2, 942–955. Claremont, New Hampshire, Claremont Manufacturing Company.

Blaker, M.R. & Peel, J.S. 1997: Lower Cambrian trilobites from North Greenland. Meddelelser om Grønland, Geoscience 35, 145 pp. https://doi.org/10.1017/s0016756898258432

Bordonaro, O.L., Pratt, B.R. & Robledo, V. 2013: Systematic, morphometric and palaeobiogeographic study of *Blainia gregaria* Walcott, 1916 (Trilobita, Ptychopariida), Middle Cambrian of the Precordillera of western Argentina. Geological Journal 48, 126–141. https://doi.org/10.1002/gj.1344

Brock, G.A. 1998: Middle Cambrian articulate brachiopods from the southern New England Fold belt, eastern Australia. Journal of Paleontology 72, 604–618. https://doi.org/10.1017/S0022336000040336

Cooper, G.A. 1951: New brachiopods from the Lower Cambrian of Virginia. Journal of the Washington Academy of Sciences 41, 4–8.

Duméril, A.M.C. 1806: Zoologie analytique, ou méthode naturelle de classification des animaux, 344 pp. Paris: Allais.

Geyer, G. & Peel, J.S. 2011; The Henson Gletscher Formation, North Greenland, and its bearing on the global Cambrian Series 2–Series 3 boundary. Bulletin of Geosciences 86, 465–543. https://doi.org/10.3140/bull.geosci.1252

Hall, J. 1859: Trilobites of the shales of the Hudson River Group. Twelfth Annual Report of the Regents of the University of the State of New York, on the condition of the State Cabinet of Natural History, and the Historical and Antiquarian Collection connected therewith, 59–62.

Hall, J. 1861: Supplementary note to the thirteenth report of the Regents of the State Cabinet: 15th Annual Report of the New York State Cabinet for Natural History 1862, 113–119.

Higgins, A.K., Ineson, J.R., Peel, J.S., Surlyk, F. & Sønderholm, M. 1991a: Lower Palaeozoic Franklinian Basin of North Greenland. Bulletin Grønlands Geologiske Undersøgelse 160, 71–139. https://doi.org/10.34194/bullggu.v160.6714

Higgins, A.K., Ineson, J.R., Peel, J.S., Surlyk, F.S. & Sønderholm, M. 1991b: Cambrian to Silurian basin development and sedimentation, North Greenland. In: Trettin, H.P. (ed.) Geology of the Innuitian Orogen and Arctic Platform of Canada and Greenland. Geology of Canada 3, 109–161. Geological Survey of Canada, Ottawa. https://doi.org/10.1130/DNAG-GNA-E.109

Holmer, L.E., Kebria-Ee Zadeh, M., Popov, L.E., Ghobadi Pour, M., Alvaro, J., Hairapetian, V. & Zhang, Z. 2019: Cambrian rhynchonelliform nisusioid brachiopods: phylogeny and distribution. Papers in Palaeontology 5, 559–575. https://doi.org/10.1002/spp2.1255

Ineson, J.R. & Peel, J.S. 1997: Cambrian shelf stratigraphy of North Greenland. Geology of Greenland Survey Bulletin 173, 120 pp. https://doi.org/10.34194/ggub.v173.5024

Keller, M., Buggisch, W. & Lehnert, O. 1998: The stratigraphical record of the Argentine Precordillera and its plate-tectonic background. The Proto-Andean Margin of Gondwana. Geological Society, London, Special Publication 142, 35–56. https://doi.org/10.1144/GSL.SP.1998.142.01.03

Kobayashi, T. 1935: The Cambro-Ordovician formations and faunas of south Chosen. Palaeontology. Part 3. Cambrian faunas of south Chosen with a special study of the Cambrian trilobite genera and families. Journal of the Faculty of Science, Imperial University of Tokyo, Section 2, 4, 49–344.

Kuhn, O. 1949: Lehrbuch der Paläozoologie, E, 326 pp. Stuttgart: Schweizerbart.

Mao, Y.Q., Zhao, Y.L., Wang, C.W. & Topper, T. 2017: A fresh look at *Nisusia* Walcott, 1905 from the Cambrian Kaili Formation in Guizhou. Palaeoworld, 26, 12–24.

Marek, L. 1963: New knowledge on the morphology of Hyolithes: Sborník Geologických věd, řada Paleontologie 1, 53–72.

Oh, Y., Lee, D., Lee , S., Lee, S., Hong, P.S. & Hong, J. 2022: Palaeobiogeography of the family Nisusiidae (Cambrian rhynchonelliform brachiopods) using the 'area-transition count' method and systematic revision of Korean species. Papers in Palaeontology 8, 1. https://doi: 10.1002/spp2.1420

Oh, Y., Peel, J.S., Zhen, Y.Y., Smith, P., Lee, M. & Park, T.S. 2024: Periostracum in Cambrian helcionelloid and rostroconch molluscs: comparison to modern taxa. Lethaia 57, 1–17. https://doi.org/10.18261/let.57.1.6

Palmer, A.R. 1957: Ontogenetic development of two olenellid trilobites. Journal of Paleontology 31, 105–128.

Palmer, A.R. 1998: Terminal Early Cambrian extinction of the Olenellina: Documentation from the Pioche Formation, Nevada. Journal of Paleontology 72, 650–672. https://doi.org/10.1017/S0022336000040373

Peel, J.S., Streng, M., Geyer, G., Kouchinsky, A. & Skovsted, C.B. 2016: *Ovatoryctocara granulata* assemblage (Cambrian Series 2–Series 3 boundary) of Løndal, North Greenland. Australasian Palaeontological Memoirs 49, 241–282.

Popov, L.E. & Tikhonov, Yu.A. 1990: Rannekembriyskiye brakhiopody iz Yuzhnoy Kirgizii [Early Cambrian brachiopods from southern Kirgizia]. Paleontologicheskiy Zhurnal 1990 (3), 33–46.

Popov, L., Holmer, L.E., Rowell, A.J. & Peel, J.S. 1997: Early Cambrian brachiopods from North Greenland. Palaeontology 40, 337–354.

Poulsen, C. 1932: The Lower Cambrian faunas of East Greenland. Meddelelser om Grønland 87(6), 66 pp.

Poulsen, C. 1958: Contribution to the palaeontology of the Lower Cambrian Wulff River Formation. Meddelelser om Grønland 162(2), 27 pp.

Pratt, B.R. & Bordonaro, O.L. 2014: Early middle Cambrian trilobites from the La Laja Formation, Cerro El Molle, Precordillera of western Argentina. Journal of Paleontology 88, 906–924. https://doi.org/10.1666/13-083

Rasetti, F. 1948: Lower Cambrian trilobites from the conglomerates of Quebec (exclusive of the Ptychopariidea). Journal of Paleontology 22, 1–24.

Resser, C.E. 1938: Cambrian System (restricted) of the southern Appalachians. Geological Society of America Special Paper 15, 140 pp. https://doi.org/10.1130/spe15

Richter, R. 1932: Crustacea (Paläontologie). Handwörterbuch der Naturwissenschaften, 2nd edition 2, 840–864.

Schuchert, C. 1893: Classification of the Brachiopoda. American Geologist 11, 141–167.

Shaw, A.B. 1954: Lower and lower middle Cambrian faunal succession in northwestern Vermont. Bulletin of the Geological Society of America 65, 1033–1406. https://doi.org/10.1130/0016-7606(1954)65[1033:LALMCF]2.0.CO;2

Shaw, A.B. 1955: Paleontology of northwestern Vermont. V. The lower Cambrian fauna. Journal of Paleontology 29, 775–805.

Siebold, C.T. von 1848: Lehrbuch der vergleichenden Anatomie der wirbellosen Thiere. Erster Theil. In: Siebold, C.T. von & Stannius, H. (eds): Lehrbuch der vergleichenden Anatomie, 679 pp. Berlin: Veit. https://doi.org/10.5962/bhl.title.10707

Skovsted, C.B. & Holmer, L.E. 2005: Early Cambrian brachiopods from North-East Greenland. Palaeontology 48, 325–345. https://doi.org/10.1111/j.1475-4983.2005.00450.x

Streng, M., Butler, A.D., Peel, J.S., Garwood, R.J. & Caron, J-B. 2016: A new family of Cambrian rhynchonelliformean brachiopods (Order Naukatida) with an aberrant corallike morphology. Palaeontology 59, 269–293. https://doi: 10.1111/pala.12226

Sundberg, F.A. & Webster, M. 2022: "Ptychoparioid" trilobites of the Harkless Formation and Mule Spring Limestone (Cambrian Series 2, Stage 4), Clayton Ridge, Nevada. Journal of Paleontology 96, 886–920. https://doi: 10.1017/jpa.2021.124

Swinnerton, H.H. 1915: Suggestions for a revised classification of trilobites. Geological Magazine (n.s.), 6, 487–496, 538–545.

Syssoiev, V.A. 1957: To the morphology, systematics and systematic position of the Hyolithoidea. Doklady Akademiya Nauk SSSR 116, 304–307. [in Russian]

Walch, J.E.I. 1771: Die Naturgeschichte der Versteinerungen, zur Erläuterung der Knorrischen Sammlung von Merkwürdigkeiten der Natur, v. 4, 3, 184 pp. Nürnburg: Paul Jonathan Felstecker.

Walcott, C.D. 1886: Second contribution to the studies of the Cambrian faunas of North America. U.S. Geological Survey Bulletin 30, 369 pp. https://doi.org/10.5962/bhl.title.38399

Walcott, C.D. 1889: Description of new genera and species of fossils from the middle Cambrian. Proceedings of the U.S. National Museum 11, 441–446. https://doi.org/10.5479/si.00963801.11-738.441

Walcott, C.D. 1890: The fauna of the lower Cambrian or Olenellus Zone. Tenth Annual Report of the Director, 1888–1889, United States Geological Survey, 509–774.

Walcott, C.D. 1905: Cambrian Brachiopoda with descriptions of new genera and species. Proceedings of the United States National Museum 28, 227–337. https://doi.org/10.5479/si.00963801.1395.227

Walcott, C.D. 1908: Cambrian Brachiopoda: descriptions of new genera and species. Smithsonian Miscellaneous Collections 53, 53–137.

Walcott, C.D. 1912: Cambrian Brachiopoda: Monograph of the United States Geological Survey 51, 872 pp. https://doi.org/10.5962/bhl.title.45577.

Walcott, C.D. 1916; Cambrian geology and paleontology III, no. 5. Cambrian trilobites. Smithsonian Miscellaneous Collections 64, 303–456.

Webster, M. 2015: Ontogeny and intraspecific variation of the early Cambrian trilobite *Olenellus gilberti*, with implications for olenelline phylogeny and macroevolutionary trends in phenotypic canalization, Journal of Systematic Palaeontology 13, 1–74. https://doi 10.1080/14772019.2013.852903

White, C.A. 1874: Preliminary report upon invertebrate fossils collected by the expeditions of 1871, 1872, and 1873, with descriptions of new species. U. S. Geographic and Geologic Surveys West of the 100th Meridian Report, 5–27.

Whitfield, R.P. 1884: Notice of some new species of Primordial fossils in the collections of the museum, and corrections of previously described species. Bulletin of the American Museum of Natural History 1 (1881–1886), 139–154.

Williams, A., Carlson, S.J., Brunton, C.H.C., Holmer, L.E. & Popov, L.E. 1996: A supra-ordinal classification of the Brachiopoda. Philosophical Transactions of the Royal Society of London (Series B), 351, 1171–1193. https://doi.org/10.1098/rstb.1996.0101