A bradoriid arthropod from the Wuliuan (middle Cambrian) of North Greenland turns phosphatocopid

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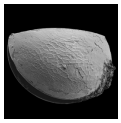

The bradoriid *Liangshanella*? *qassutit* Peel, 2025 from the middle Cambrian (Wuliuan Stage; *Ptychagnostus gibbus* Biozone) upper Henson Gletscher Formation of North Greenland is recognized as a phosphatocopid. Reinvestigation of the only known specimen revealed the presence of a doublure and an interdorsum denoting its phosphatocopid affinity. The broad, lens-shaped interdorsum indicates correspondence with the genus *Comleyopsis* Hinz, 1993 of the family Hesslandonidae Müller, 1964 and the taxon is accordingly re-described as *Comleyopsis qassutit* (Peel, 2025) comb. nov. The species from North Greenland is most similar with the contemporary *Comleyopsis iecta* Hinz-Schallreuter & Koppka, 1996 from northern Germany and the two species represent the youngest occurrences of the genus. A single phosphatocopid specimen illustrated as *Hesslandona* sp. by Zhang & Pratt, 2012 from the early Cambrian of China has an interdorsum characteristic for *Comleyopsis* and is interpreted to represent a new, yet undescribed species of the genus. The Chinese specimen represents the oldest occurrence of the genus. • Key words: Phosphatocopida, Bradoriida, *Liangshanella*, *Comleyopsis*, middle Cambrian, Wuliuan, North Greenland.

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The taxa Bradoriida Raymond, 1935 and Phosphatocopida Müller, 1964 accommodate an expansive diversity of smaller bivalved arthropods which had their prime during the Cambrian. Whereas the bradoriids are millimetres to up to nearly 2 cm in length, phosphatocopids are typically much smaller ranging from a few 100 µm to not more than 3 mm, although rare lengths of 5 mm (Williams *et al.* 1994) and even up to 9.3 mm (Hinz-Schallreuter 2000) have been reported for one species. All phosphatocopids are characterized by an inward fold of the outer carapace layer, the so called doublure (= duplicature of some authors, *e.g*. Williams & Siveter 1998, Zhang & Pratt 2012) and in most species a narrow plate, the interdorsum, is developed between the two valves of their carapaces. A doublure and interdorsum are not developed in bradoriids although for some species a narrow duplicature has been mentioned (*e.g.* Zhang 2007). Phosphatocopids are generally considered as a monophyletic group representing the sister-group to crown-crustaceans (Eucrustacea) (Maas *et al.* 2003, Siveter *et al.* 2003, Waloszek 2003), whereas the Bradoriida with their diversity of simple-hinged bivalved carapaces might be polyphyletic stem-Crustacea (but see Zhai *et al.* 2019). Bradoriids are common and diverse during the early and middle Cambrian and decline during the late Cambrian, which is opposite to the development of the phosphatocopids that are uncommon and low in diversity in early and early middle Cambrian rocks before they diversify at the end of the Drumian Stage (Williams *et al*. 2011, Reynolds *et al.* 2025).

From this transitional time, the late middle Cambrian, Peel (2025) recognized a single specimen of a bivalved arthropod carapace and described it as *Liangshanella*? *qassutit*. Accommodation of the new taxon in the bradoriid genus *Liangshanella* was at the time arbitrary as the specimen's admarginal brim is minute contrasting the distinct admarginal structures characteristic for the genus. Furthermore, the carapace of the specimen has an ornamentation unknown from other species of *Liangshanella*. A comparison with the phosphatocopids was precluded as the specimen seemingly lacked a doublure (Peel 2025). During a reinvestigation of the specimen in the course of a review of the described species of *Liangshanella* (Streng, unpublished data), the presence of a doublure and an interdorsum was revealed, denoting that the specimen is in fact a phosphatocopid. Accordingly, the specimen is herein re-described as a phosphatocopid. The broad, lens-shaped interdorsum indicates reference to the genus *Comleyopsis* Hinz, 1993 of the family Hesslandonidae.

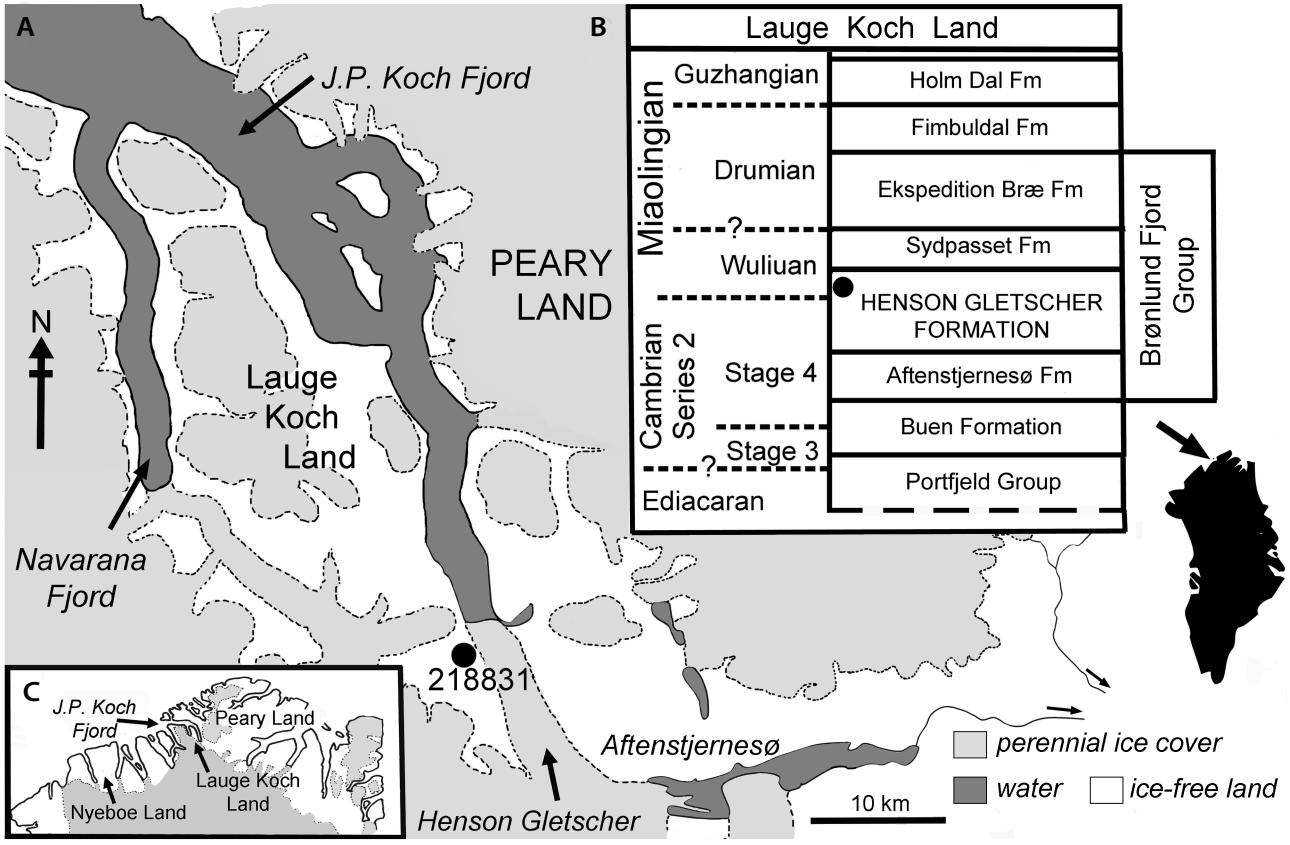

Figure 1. Locality and stratigraphic context for *Comleyopsis qassutit* (Peel, 2025) comb. nov. • A – collection site for GGU sample 218831 containing *C. qassutit* in southern Lauge Koch Land. The area's major fjord, J.P. Koch Fjord, is located by arrow in inset map of Greenland.• B – Cambrian stratigraphy in southern Lauge Koch Land with black dot indicating stratigraphic position of sample 218831 within the upper Henson Gletscher Formation. • C – map of North Greenland, with ice cover shaded. Figure modified after Peel (2023, fig. 1).

Locality and age

The re-described specimen originates from GGU sample 218831 collected in the upper Henson Gletscher Formation as exposed at its type locality in southern Lauge Koch Land, North Greenland (Fig. 1; for further details on locality see Peel 2023, 2025). Co-occurring agnostids indicate the *Ptychagnostus gibbus* Biozone of the late Wuliuan (see Peel 2025 for details). The specimen of *Flumenoglacies* sp. nov. illustrated herein for comparison (Fig. 2I), is from the basal Burgess Shale Formation (Wuliuan) as exposed in the Marble Canyon area, Kootenay National Park, British Columbia, Canada.

Methods and depository

The specimen (PMU 39671) was previously studied and photographed using a scanning electron microscope (SEM) (Peel 2023, 2025). Re-investigation of the specimen revealed its accidental damage during storage, which required a re-coating of the now crushed carapace for further SEM analysis. The remains were sputter-coated with an alloy of gold and palladium and then photographed using a Zeiss Supra 35VP field emission SEM at the Department of Earth Sciences, Uppsala University. The same methods apply to the specimen of *Flumenoglacies* sp. nov. (ROMIP69694). The specimen of *C. qassutit* is housed in the collections of the Museum of Evolution, Uppsala University, Sweden (acronym PMU) and *Flumenoglacies* sp. nov. is part of the Invertebrate Palaeontology collections of the Royal Ontario Museum, Toronto, Canada (acronym ROM).

Systematic palaeontology

Order Phosphatocopida Müller, 1964
Family Hesslandonidae Müller, 1964

Diagnosis. – Phosphatocopids with small, amplete to elongate preplete valves and a broad to narrow interdorsum. Up to three subdorsally situated nodes in larger juveniles

and adults. Lateral surface smooth or with a pattern of polygons (modified after Williams & Siveter 1998).

Discussion. – The diagnosis of Williams & Siveter (1998) only considered smooth lateral surfaces of the carapace. It is here extended with the possibility of ornamented lateral surfaces as seen in *Comleyopsis qassutit* comb. nov.

Genus *Comleyopsis* Hinz, 1993

Type species. – *Comleyopsis schallreuteri* Hinz, 1993 from the *Strenuella* Limestone, Comley Series, Shropshire, England. Locality 2 of Cobbold (1927); horizon Ac4 of Cobbold (1921), which belongs to the *Strenuella sabulosa* Biozone, the basal zone of Cambrian Stage 4 following Harvey *et al.* (2011).

Other species included. – *Comleyopsis iecta* Hinz-Schallreuter & Koppka, 1996 from a limestone erratic, northern Germany, Wuliuan Stage (?*Ptychagnostus gibbus* Zone); *Liangshanella*? *qassutit* Peel, 2025 from the Henson Gletscher Formation, North Greenland, Wuliuan Stage (*Ptychagnostus gibbus* Zone) (re-described below).

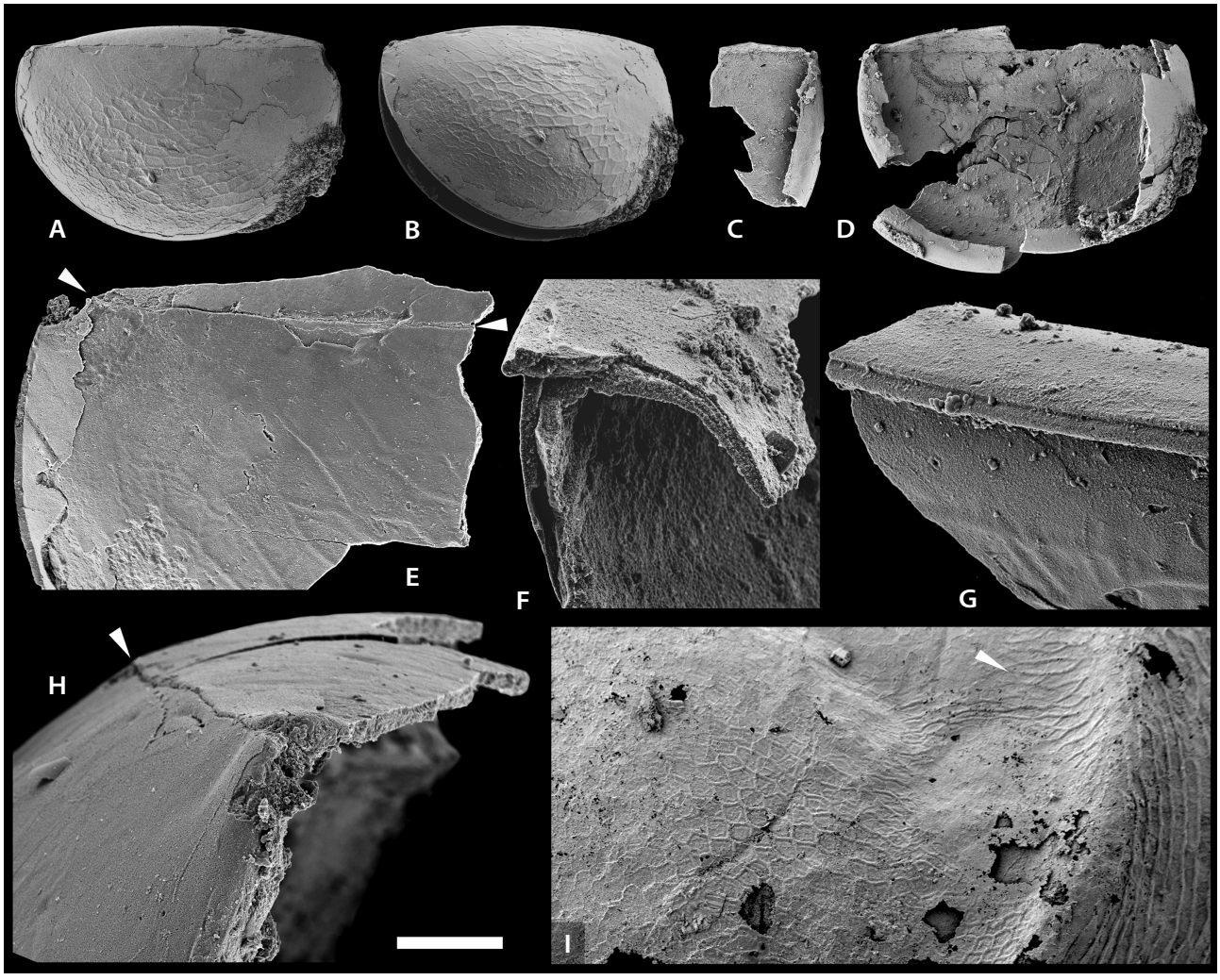

Figure 2. A–H – *Comleyopsis qassutit* (Peel, 2025) comb. nov. (holotype, PMU 39671) from the upper Henson Gletscher Formation, North Greenland (late Wuliuan), before (A, B) and after damage of the specimen (C–H). A, B – lateral and oblique lateral view of carapace showing lens shaped interdorsum (A) and polygonal ornamentation (A, B). C, D – internal view of the two valves showing doublure; note suture between valve and interdorsum in each valve. E – same fragment as in C in external view showing concave indentation at cardinal corner; suture between valve and interdorsum marked by arrows. F – cross section of valve margin showing narrow brim and internally tapering doublure. G – ventral valve margin with brim and fine groove separating doublure from brim. H – axial view of valve with remnants of interdorsum, opposing part to E, suture between valve and interdorsum marked by arrow. • I – outer surface of bradoriid *Flumenoglacies* sp. nov. (specimen ROMIP69694) from the Burgess Shale Formation (Wuliuan), Kootenay National Park, British Columbia, Canada, showing comparable ornamentation to *C. qassutit*; note elongated polygons (arrow). Scale bar equals 150 µm (A–D), 40 µm (E), 15 µm (F, G), 20 µm (H), and 75 µm (I).

Diagnosis. – Hesslandonid with small (*ca*. 500 µm in length), amplete to subamplete valves with broad, lens-shaped interdorsum. Interdorsum with an anterior and posterior spine, which might be distinct to rudimentary. Outer surface without lobation.

Discussion. – The type species of *Comleyopsis* was commonly considered to be a juvenile due to its small size (Williams & Siveter 1998, Siveter *et al.* 2003), but all specimens currently placed within the genus, although limited in number (n = 5), have an equivalent small size suggesting that *Comleyopsis* is potentially a genus accommodating "small" species. The specimen of *Hesslandona* sp. of Zhang & Pratt (2012), herein considered a new, undescribed species of *Comleyopsis*, is with a length of *ca*. 600 µm the largest known specimen of *Comleyopsis*. The specimen is from the early Cambrian (Cambrian Stage 3) Shuijingtuo Formation in Zhenba County, Shaanxi, China, and was only illustrated and not described by Zhang & Pratt (2012, fig. 1k). With its broad, lens-shaped interdorsum featuring a prominent anterior and posterior spine, its carapace appears to be analogous to *Comleyopsis schallreuteri*. It differs in outline in having smaller cardinal angles, resulting in a less pronounced anterior and posterior margin in comparison to *C. schallreuteri*. *Hesslandona* sp. represents the oldest occurrence of the genus *Comleyopsis*.

It is noteworthy that *Comleyopsis* currently accommodates two morphotypes. The two early Cambrian representatives of the genus, *C. schallreuteri* and *Comleyopsis* n. sp. (= *Hesslandona* sp. of Zhang & Pratt 2012), differ distinctly from the two middle Cambrian forms, *C. iecta* and *C. qassutit* comb. nov., in the expression of their interdorsa. Whereas the early forms have an interdorsum with prominent spines, the later forms seemingly have either only rudimentary spines or lack them entirely. Additional material might show that the two stratigraphically separated morphotypes could represent discrete genera.

Occurrence. – Cambrian Stage 3 to late Wuliuan (*Ptychagnostus gibbus* Biozone) of England, Scandinavia, North Greenland and China.

***Comleyopsis qassutit* (Peel, 2025) comb. nov.**
Figure 1A–H

2023 Bradoriid in lateral view. – Peel, p. 106, fig. 5a.
2025 *Liangshanella*? *qassutit* sp. nov.; Peel, pp. 18, 19, fig. 12a–c.

Material. – Known only from the holotype (PMU 39671 from GGU sample 218831) of Peel (2025), which since has been damaged during storage; upper Henson Gletscher Formation, southern Lauge Koch Land, North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage.

Diagnosis. – Amplete species of *Comleyopsis* with interdorsum lacking distinct spines; outer surface of carapace with net-like ornament of polygons. Valve length *vs.* valve height about 1.65; greatest length at about 75% of valve height from ventral margin.

Description. – Equivalved, bivalved carapace with amplete left and right valves, separated by a broad lens-shaped interdorsum. Length of carapace *ca.* 490 µm and height (= valve height, *i.e.* distance from ventral margin to suture of interdorsum) about 300 µm; maximum height at about midlength. Free margin of valves evenly rounded without distinct changes in curvature; cardinal angles between 100° and 110°, placing the maximum length of each valve at about 75% of height. Free margin of valves with narrow brim about 3.2 µm broad (Fig. 1E–G), associated with a fine groove that separates the brim from the doublure (Fig. 1G). Doublure present along the inner margin of both valves, entire between cardinal corners and of about constant width of 45 µm, except near antero- and posterodorsal corners where it tapers rapidly towards the cardinal corners (Fig. 1C, D); outer surface of doublure smooth, no ornamentation or pores have been observed (Fig. 1C, D, G). Broad, lens-shaped interdorsum about 460 µm long, with a maximum width of 115 µm at about midlength, *i.e.* interdorsum is four times longer than wide (Fig. 1A). Outer surface of valve ornamented by a polygonal network of fine ridges that fade towards the margins of the valves. Polygons have maximum diameters of *ca*. 25 to 35 µm.

Discussion. – *Comleyopsis qassutit* is most similar to *C. iecta* Hinz-Schallreuter & Koppka, 1996 from potentially coeval strata in Scandinavia. Both have an interdorsum lacking distinct spines but are seemingly easily distinguishable by the for phosphatocopids unusual net-like ornament present in *C. qassutit*, which contrasts with the typically smooth carapaces of other phosphatocopids such as *C. iecta*. Nevertheless, analogous ornamentation has been reported from some other phosphatocopids:

1) A reticulostriate ornament was mentioned and illustrated by Williams & Siveter (1998, pl. 6, figs 9, 10) for the single valve of "phosphatocopid gen. et sp. indet. F", recovered from the *bellimarginatus* limestone at Comley Quarry (*Strenuella sabulosa* Biozone of Harvey *et al.* 2011). The specimen was compared with *Dabashanella* which may have equivalent spinose cardinal corners. However, *Dabashanella* is considered to be a genus with a univalved carapace (see Zhang 2023 for review) and the nature of the dorsal margin of the single valve (!) from Comley is not known, making a taxonomic comparison problematic.

2) Zhang & Pratt (2012) reported the presence of a network of fine ridges in some specimens of their *Dabashanella* sp. and illustrate one specimen with such a feature (see Zhang & Pratt 2012, fig. 1h). The specimens of *Dabashanella* sp. illustrated by Zhang & Pratt (2012) were subsequently synonymized with *Dabashanella hemicyclica* Huo, Shu & Fu, 1983 *in* Huo *et al.* (1983) by Zhang (2023).

3) Ornamentation equivalent to the previous two examples was described by Wrona (2009) for the presumed early Cambrian *Dabashanella*? sp. 2 but here the network is made of furrows rather than ridges. Comparable polygonal patterns occur also within the bradoriids as, *e.g.* in an undescribed species of *Flumenoglacies* Peel & Streng, 2015 from the early middle Cambrian Burgess Shale Formation (Streng, unpublished data, Fig. 2I) or in several spinose taxa (see, *e.g.* Zhang 2007; Peel *et al.* 2021). In these taxa, the polygons appear more regular in shape and are generally smaller (10–20 µm), but a lateral transition into elongated polygons is also observed in *Flumenoglacies* sp. nov. (arrow in Fig. 2I). The presence of equivalent polygonal ornamentation in rather different phosphatocopid taxa, as well as its absence and presence (preservational variation?) within the same taxon as stated by Zhang & Pratt (2012) for *Dabashanella* sp., suggests a low taxonomic value for such a feature. Hence, the ornamentation of *Comleyopsis qassutit* should not be used as the only argument to distinguish it from *C. iecta*. The two species are further distinguished by their length-height ratio and their cardinal angles. The specimen of *C. qassutit* has the same length as the holotype of *C. iecta* but is with 300 µm about 30 µm taller than the latter. With cardinal angles between 100° and 110°, the outline of *C. qassutit* is more ovoid contrasting the elongate, semi-circular outline of *C. iecta* for which cardinal angles of about 90° have been reported (Hinz-Schallreuter & Koppka 1996). Additional differences might lie with the development of potential spines, but the cardinal corners are insufficiently preserved in *C. qassutit*. Still, due to the low numbers of known specimens for either species and the resulting uncertainties regarding their potential morphological variability, it cannot readily be excluded that the discussed differences could also fall within the variation of a single species.

Orientation of the amplete carapace of *C. qassutit* is not possible as indicators for posterior or anterior are missing. Lobes in hesslandonids occur preferentially in the anterodorsal region, but *Comleyopsis* is an alobate member of this family. Hinz-Schallreuter & Koppka (1996) use the slight asymmetry of the interdorsum of certain taxa for orientation where the greatest width is not medial but supposedly in the anterior half. Due to damage of the specimen and the interdorsum, such details cannot be seen in *C. qassutit*. The doublure of hesslandonids can show differences in width between anterior and posterior and it is the posterior part that typically is broader (Maas *et al.* 2003). However, the carapace remains of *C. qassutit* do not show any distinct differences in the width of the doublure that would facilitate an orientation. The small concave indentation at one of the cardinal corners (Fig. 1E), interpreted by Peel (2025) as a broken off anterior spine appears to be not developed on the opposite end of the valve. However, the opposite cardinal corner appears damaged showing an even larger concave indentation (Fig. 1A) potentially disguising a corresponding structure. The nature of these indentations and their relation to potential former spines is currently unclear.

Acknowledgements

The sample with *C. qassutit* was collected by J.S. Peel during fieldwork which was part of North Greenland Project (1979–80) organised by the Geological Survey of Greenland (GGU). The specimen of *Flumenoglacies* sp. nov. comes from a sample collected in Kootenay National Park (British Columbia, Canada) by M. Streng in 2016 during exploration conducted by the Royal Ontario Museum (ROM) under a Parks Canada Collection and Research Permit to Jean-Bernard Caron (ROM). We thank A. Gerbe and an anonymous reviewer for their comments and suggestions on the submitted manuscript.

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