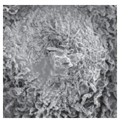
A priapulid larva from the middle Cambrian (Wuliuan Stage) of North Greenland (Laurentia)

John S. Peel



A single phosphatised specimen from the middle Cambrian Henson Gletscher Formation (Miaolingian Series, Wuliuan Stage) of North Greenland is interpreted as the hatching larva of a total-group priapulid worm. A plated lorica is not present but probably was developed at a later larval stage, by comparison with the described development of extant *Priapulus caudatus* and *Halicryptus spinulosus*. A characteristic priapulid introvert with scalids is not seen but it was likely withdrawn in the available specimen. The new find is consistent with a similar ontogeny in Cambrian priapulid cycloneuralians to that seen in their present day relatives. New taxon: *Inuitiphlaskus kouchinskyi* gen. et sp. nov. • Key words: total-group priapulid, larva, Cambrian, Miaolingian (Wuliuan), North Greenland, Laurentia.

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Present day priapulids comprise a small group of cycloneuralian worms containing only about 22 described species (Maas 2013, Schmidt-Rhaesa 2013, Hejnol 2015, Schmidt-Rhaesa *et al.* 2017, Schmidt-Rhaesa & Freese 2019). Most species are small and live infaunally, commonly as meiofauna, but Shirley & Storch (1999) described specimens that attained a length of 39 cm.

Priapulids have a poor geological record but stem-group priapulids are diverse in lower and middle Cambrian Lagerstätten, and were referred to as archaeopriapulids by Conway Morris (1977). Well preserved burrows attributed to priapulids have also been described from Cambrian (Series 2) sandstones in Sweden (Kesidis *et al.* 2019) and similar claims are known from the Ediacaran (Turk *et al.* 2022).

The oldest priapulid-like worm, *Eopriapulites* Liu & Xiao, 2014 *in* Liu *et al.* (2014), and other scalidophoran worms were described from the early Cambrian (Fortunian) of China by Liu *et al.* (2014, 2019), Shao *et al.* (2016a, b; 2020a, b) and Zhang (2022). Yang *et al.* (2016) noted 17 species assigned to 16 genera from the Chengjiang Lagerstätte (Cambrian Series 2) of southern China and five species referred to five genera from the middle Cambrian (Miaolingian Series) Burgess Shale of British Columbia (Conway Morris 1977, Briggs *et al.* 1994, Vannier 2012, Smith *et al.* 2015).

A single stem-group priapulid species, *Singuuriqia simoni* Peel, 2017 has been described from the Sirius Passet Lagerstätte (Cambrian Series 2) of North Greenland (Peel 2017). Note that at the time of writing, a reference to *Singuuriqia cristatus* (Agassiz, 1844) [actually published as Agassiz 1845, see revision in Monsch 2005] as a perciformean fish occurs in several online databases. The records appear to be a simple error. The name *Singuuriqia* does not appear in the referenced publications and a homonym of *Singuuriqia* Peel, 2017 is not known.

The relationship between Cambrian and Recent priapulid worms and other cycloneuralians (palaeoscolecidan worms, loriciferans, kinorhynchs, nematomorphans and nematodes), some of which show similar time distributions, is uncertain. Wills *et al.* (2012) considered that archaeopriapulids and present day priapulids shared a paraphyletic relationship with each other. Nielsen (1995) considered that the development of a lorica, a corset of plates arranged longitudinally around the trunk, was a unifying character for priapulids and loriciferans, as Vinctiplicata, but the traditional relationship between priapulids, loriciferans and kinorhynchs within Scalidophora has been questioned. Some authors have placed Loricifera as a sister group to Nematomorpha on morphological and molecular grounds (Sørensen *et al.* 2008, Peel 2010a, Peel *et al.* 2013, Yamasaki *et al.* 2015), especially noting the hexaradial symmetry of buccal structures in loriciferans and nematomorphans (Sørensen *et al.* 2008, Peel 2010a, Peel *et al.* 2013), although, this relationship was rejected by Maas *et al.* (2013). However, Peel (2010a) and Peel *et al.* (2013) considered that circumoral, multicuspidate, hexaradially disposed, grasping denticles in the lorica of *Sirilorica* Peel, 2010a from the Sirius Passet Lagerstätte (Cambrian Series 2) of North Greenland emphasised the relationship between these Cambrian fossils and living

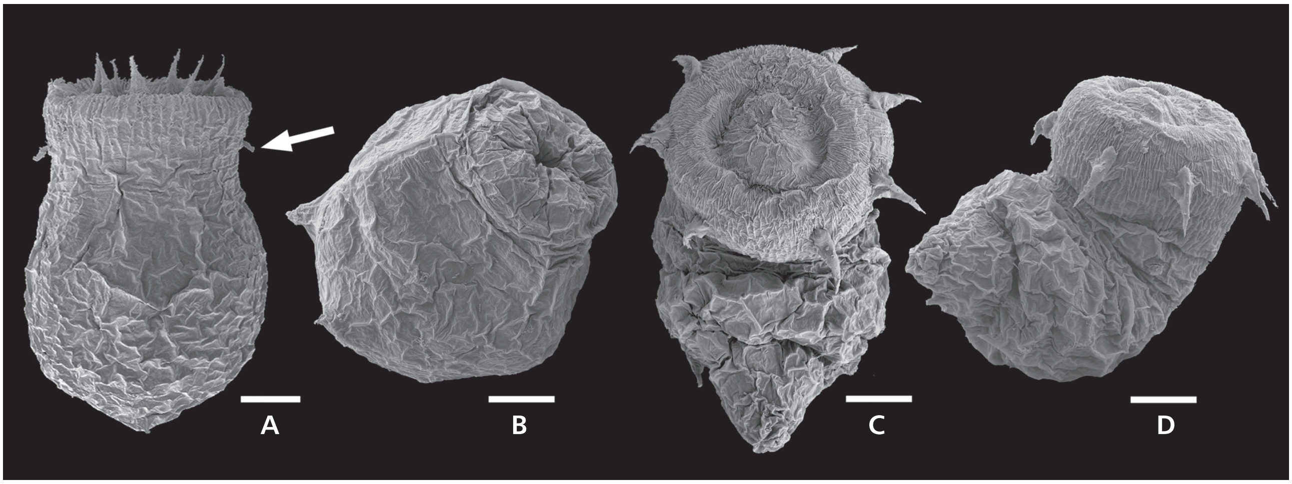

Figure 1. Hatching larvae of present day priapulids. • A – *Priapulus caudatus* Lamarck, 1816, larva in lateral view with slightly everted anterior introvert carrying scalids, and lateral tubuli in the neck region (arrow). Parent specimens were collected from Gullmars Fjord, south-west Sweden, in the vicinity of Kristineberg Marine Research Station (University of Gothenburg). • B–D – *Halicryptus spinulosus* Siebold, 1849; B – larva with fully retracted introvert, anterior to upper right; C – hatching larvae with everted introvert carrying seven peripheral first ring scalids, anterior up; D – same specimen as in C, viewed laterally. Parent specimens were collected from the Baltic Sea in the vicinity of the Askö laboratory (Stockholm University Baltic Sea Centre), on the south-east coast of Sweden. Scale bars: 20 µm. Photographs by Sofia A. Wennberg, originally published in Janssen *et al.* (2009) and Wennberg *et al.* (2009).

loriciferans and nematomorphans. As a consequence, Peel *et al.* (2013) considered that the development of a lorica was not a unifying character for priapulids and loriciferans within Vinctiplicata, noting in passing the morphological similarity between the loricas of *Sirilorica* and the present day rotifer *Notholca ikaitophila* Sørensen & Kristensen, 2000. Hejnol (2015) considered the resemblance of loriciferans to priapulid loricate larvae to be superficial. Shao *et al.* (2016a) suggested that similar buccal structures in *Eopriapulites*, interpreted as a stem-group scalidophoran, indicated that hexaradial symmetry was developed independently in nematoid nematomorphans and *Eopriapulites*.

Priapulid development

Almost all priapulids develop from eggs to the adult by way of a larval form that is stiffened by a lorica consisting of several longitudinal plates. Schmidt-Rhaesa & Freese (2019) stressed the incomplete state of knowledge concerning the larval development of priapulids. They listed published records concerning the loricate larva in 11 of the 22 recognised species (Schmidt-Rhaesa & Freese 2019, table 1), but noted that an earlier growth stage, a hatching larva without lorica, was currently known in two species, *Priapulus caudatus* Lamarck, 1816 and *Halicryptus spinulosus* Siebold, 1849, as described by Wennberg *et al.* (2009) and Janssen *et al.* (2009), respectively (Fig. 1).

A single available specimen described herein from the upper Henson Gletscher Formation of North Greenland (Fig. 2) is interpreted as a probable hatching larva of a total-group priapulid (Fig. 3) due to its close similarity to larvae in the present day *Priapulus caudatus* and *Halicryptus spinulosus* (Janssen *et al.* 2009, Wennberg *et al.* 2009). Information concerning later growth stages than the hatching larva is lacking in the Henson Gletscher Formation specimen. However, the unique specimen is formally described as *Inuitiphlaskus kouchinskyi* gen. et sp. nov. on account of its much larger size than the morphologically similar present day material described by Janssen *et al.* (2009) and Wennberg *et al.* (2009), and its great antiquity (middle Cambrian, Miaolingian Series, Wuliuan Stage; 506–510 my).

Background and methods

I collected GGU sample 271492 (Fig. 2) from Cambrian strata (Miaolingian Series, Wuliuan Stage, *Ptychagnostus gibbus* Biozone) of the Henson Gletscher Formation on 25th June 1978 while participating in the North Greenland Project (1978–1980), a regional mapping program of Grønlands Geologiske Undersøgelse (Geological Survey of Greenland). The sample is derived from 56.5 m above the base of the Henson Gletscher Formation (thickness 62 m) at its type locality in south-east Lauge Koch Land (Fig. 2A; 82°10′ N, 40° 24′ W) in scours on the top of a 1 m thick mass flow deposit (Ineson & Peel 1997, fig. 31; Geyer & Peel 2011, fig. 3; Peel & Kouchinsky 2022, fig. 2a).

The Henson Gletscher Formation in the Lauge Koch Land – western Peary Land region of North Greenland

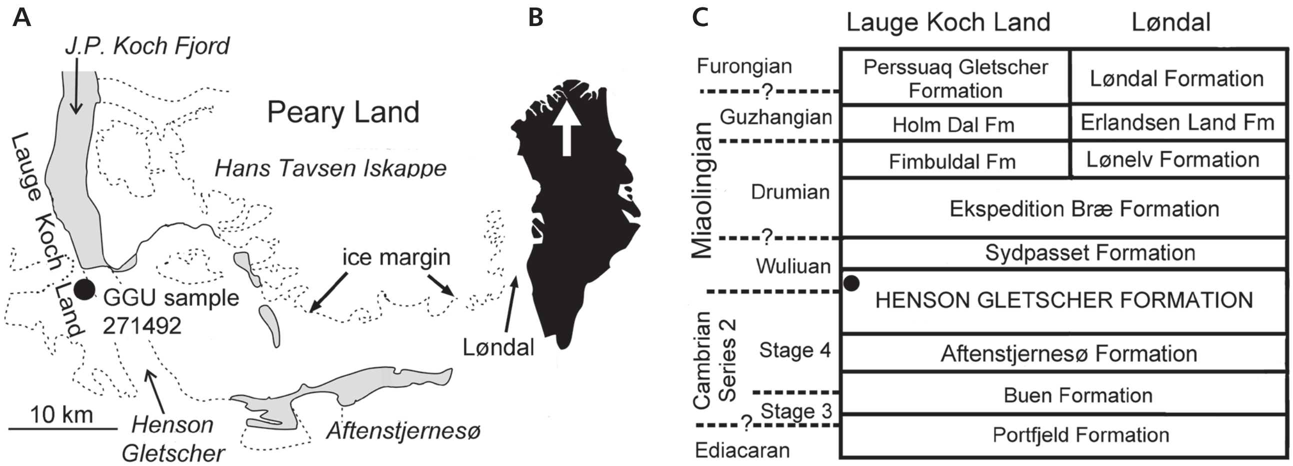

Figure 2. Geographical and geological information. • A – collection locality for GGU sample 271492 in Lauge Koch Land. • B – Greenland showing location of J.P. Koch Fjord and Henson Gletscher (arrow). • C – Cambrian stratigraphy in the Lauge Koch Land and Løndal regions showing stratigraphic derivation of GGU sample 271492 (black dot).

(Fig. 2) forms part of a prograding complex of shelf carbonates and siliciclastic sediments (Higgins *et al.* 1991, Ineson & Peel 1997, Geyer & Peel 2011, Peel *et al.* 2016). It is dominated by dark, recessive, bituminous and cherty limestones, dolostones and mudstones, although a middle member is composed of pale fine-grained sandstones. Thin carbonate debris flows occur sporadically. The formation is highly fossiliferous, with assemblages in southern Lauge Koch Land and Løndal (Fig. 2A) ranging in age from Cambrian Series 2 (Stage 4) to the Miaolingian Series (Wuliuan Stage; *Ptychagnostus gibbus* Biozone). Drumian Stage strata occur to the west along the northern coast of North Greenland (Higgins *et al.* 1991; Robison 1984, 1994; Babcock 1994; Blaker & Peel 1997; Ineson & Peel 1997; Geyer & Peel 2011). Trilobite faunas from the Henson Gletscher Formation have a dominantly Laurentian character but the assemblages include cosmopolitan agnostoids and other taxa that are important for international correlation with Siberia, the Altai Sayan foldbelt and South China (Babcock 1994, Robison 1994, Blaker & Peel 1997, Geyer & Peel 2011). Elements of the diverse associated fauna were described by Clausen & Peel (2012), Peel *et al.* (2016), Peel (2017, 2019, 2021, 2022) and Peel & Kouchinsky (2022).

Methods. – The carbonate sample was dissolved in weak acetic acid and wet sieved in fractions (125 µm and coarser) before examination under a binocular microscope. Selected specimens were gold coated prior to scanning electron microscopy. Images were assembled in Adobe Photoshop CS4.

Repositories and institutional abbreviations. – The prefix GGU indicates a sample collected by Grønlands Geologiske Undersøgelse (Geological Survey of Greenland), now a part of the Geological Survey of Denmark and Greenland (GEUS), Copenhagen, Denmark. PMU indicates a specimen deposited in the palaeontological type collection of the Museum of Evolution, Uppsala University, Sweden.

Systematic palaeontology

This published work and the nomenclatural acts it contains have been registered in ZooBank: *https://zoobank.org/References/C51625A5-5089-420E-8B9F-D4DF46A8BFEC*

Total-group priapulid

Genus *Inuitiphlaskus* gen. nov.

Type species. – *Inuitiphlaskus kouchinskyi* sp. nov., by monotypy, from the upper Henson Gletscher Formation of Lauge Koch Land, North Greenland. Cambrian, Miaolingian Series, Wuliuan Stage.

Etymology. – From *Inuit*, the native people of the Laurentian arctic regions, and the Greek *phlaskos*, meaning flask or container, alluding to the overall shape. Masculine.

Diagnosis. – Priapulid in which the elongate, flask-shaped larva has a circular cross-section, well-developed neck and anterior rim; anterior surface with central swelling, mouth not observed. Lorica not developed at this growth stage; introvert spines not observed.

Remarks. – The flask-shaped larva of *Inuitiphlaskus* differs from hatching larvae of *Priapulus caudatus* and *Halicryptus spinulosus* in terms of its much larger size, width about 400 µm compared to about 80 µm in the morphologically similar present day material described by Janssen *et al.* (2009) and Wennberg *et al.* (2009), and its great antiquity (middle Cambrian, Miaolingian Series, Wuliuan Stage; 506–510 my). An introvert has not been observed in *Inuitiphlaskus kouchinskyi*. However, it is interpreted as being withdrawn, as is the case also in a specimen of *Halicryptus spinulosus* described by Janssen *et al.* (2009; Fig. 1B). *Inuitiphlaskus kouchinskyi* is interpreted as a hatching larva; later growth stages are not known. A lorica is not present at this growth stage and its presence is therefore omitted from the diagnosis. While the presence of a later loricate larval stage is considered likely, it is possible that direct development took place of the adult from the hatching larva, in similar fashion to the ontogeny of the present day *Meiopriapulus* Morse, 1981 (Higgins & Storch, 1991).

Orstenoloricus Maas, Waloszek, Haug & Müller, 2009, from the Monastery Creek Formation (Miaolingian, Wuliuan Stage) of Queensland, Australia, differs from *Inuitiphlaskus* in the presence of a lorica with twenty longitudinal plates (Maas *et al.* 2009) that motivated its interpretation as a loriciferan. While a lorica is not present in *Inuitiphlaskus* as currently known, post-mortal folding gives the impression of longitudinal plates on the larval surface (Fig. 3C, D, F). A lorica may have been developed in a later growth stage than that represented by the available specimen of *Inuitiphlaskus kouchinskyi*, as described in *Priapulus caudatus*, where the first loricate stage has eight longitudinal cuticular plates described by Wennberg *et al.* (2009, fig. 6a, b).

The anterior region of *Orstenoloricus* is transversely folded, concertina fashion. This folded region, located to the anterior of the lorica, was termed the neck by Maas *et al.* (2009) but in the present context 'neck' follows the usage of Wennberg *et al.* (2009) and refers to the constricted area posterior to the anterior rim (Fig. 3D). A concertina-folded anterior region (neck of Maas *et al.* 2009) is not known in *Inuitiphlaskus*.

Sicyophorus rara Luo & Hu, 1999 *in* Luo *et al*. (1999) from the Chengjiang Lagerstätte (Cambrian Series 2) displays an inflated flask-shaped trunk similar to that of *Inuitiphlaskus* but about 4 mm in width. However, it is covered with longitudinal plates of the lorica that are not present in *Inuitiphlaskus* as currently known (Maas *et al.* 2007). Additionally, a prominent introvert with abundant scalids is usually preserved in *Sicyophorus rara*. An introvert of equivalent size may be developed in *Inuitiphlaskus* at a larger growth stage than the currently available specimen. However, if present in the Greenland specimen, it is considered to be inverted and therefore not visible.

Inuitiphlaskus kouchinskyi **sp. nov.**
Figure 3

Holotype. – PMU 28893 from GGU sample 271492.

Type horizon and locality. – Upper Henson Gletscher Formation, southern Lauge Koch Land, North Greenland.

Etymology. – For Artem Kouchinsky (Stockholm) who first located the specimen and prepared initial SEM images during routine processing of my Cambrian sample residues from North Greenland.

Diagnosis. – As for the genus *Inuitiphlaskus*, by monotypy.

Description. – As preserved, this unique specimen has a length of about 1250 µm and a maximum width of 400 µm (Fig. 3C). The trunk forms about two thirds of the overall length; its posterior end is slightly eroded. The trunk is separated from the rounded anterior rim by a concave neck (Fig. 3D). The anterior surface has a raised and shallowly convex peripheral zone that becomes concave as the centre is approached. The central area is formed by a conical mound, the height of which is about one third of its diameter (Fig. 3B, I). The trunk and neck carry longitudinal ridges and grooves that terminate at the periphery of the anterior rim, but their irregularity suggests that they result mainly from postmortal deformation (Fig. 3C, D, F). The outer surface is wrinkled, with narrow ridges often forming a crude reticulate pattern (Fig. 3G). Rare circular ridges may suggest the presence of small posterior spines or tubuli (Fig. 3H, J). The wrinkled pattern is only weakly developed on the conical mound at the centre of the anterior surface (Fig. 3A, B).

Remarks. – *Inuitiphlaskus kouchinskyi* is about eight times larger than illustrated hatching larvae of present day *Priapulus caudatus* described by Wennberg *et al.* (2009; Fig. 1A). It differs from the hatching larva of *Priapulus caudatus* in terms of its more slender form, with width about one third of length compared to half in *Priapulus caudatus*. However, to some extent this difference may reflect the postmortal wrinkling of the Greenland specimen (Fig. 3C, D, F). Additionally, the neck of *Inuitiphlaskus kouchinskyi* is longer and more clearly defined than that in *Priapulus caudatus*.

A hatching larva without lorica was described by Janssen *et al.* (2009) in *Halicryptus spinosus* and it is similar in size to that of *Priapulus caudatus* (Fig. 1). As described, the hatching larvae of the two living species are similar in that they lack a mouth and pharyngeal teeth, but the larva of *Halicryptus spinosus* may display transverse flexure (Fig. 1C) not seen in *P. caudatus* (Janssen *et al.* 2009).

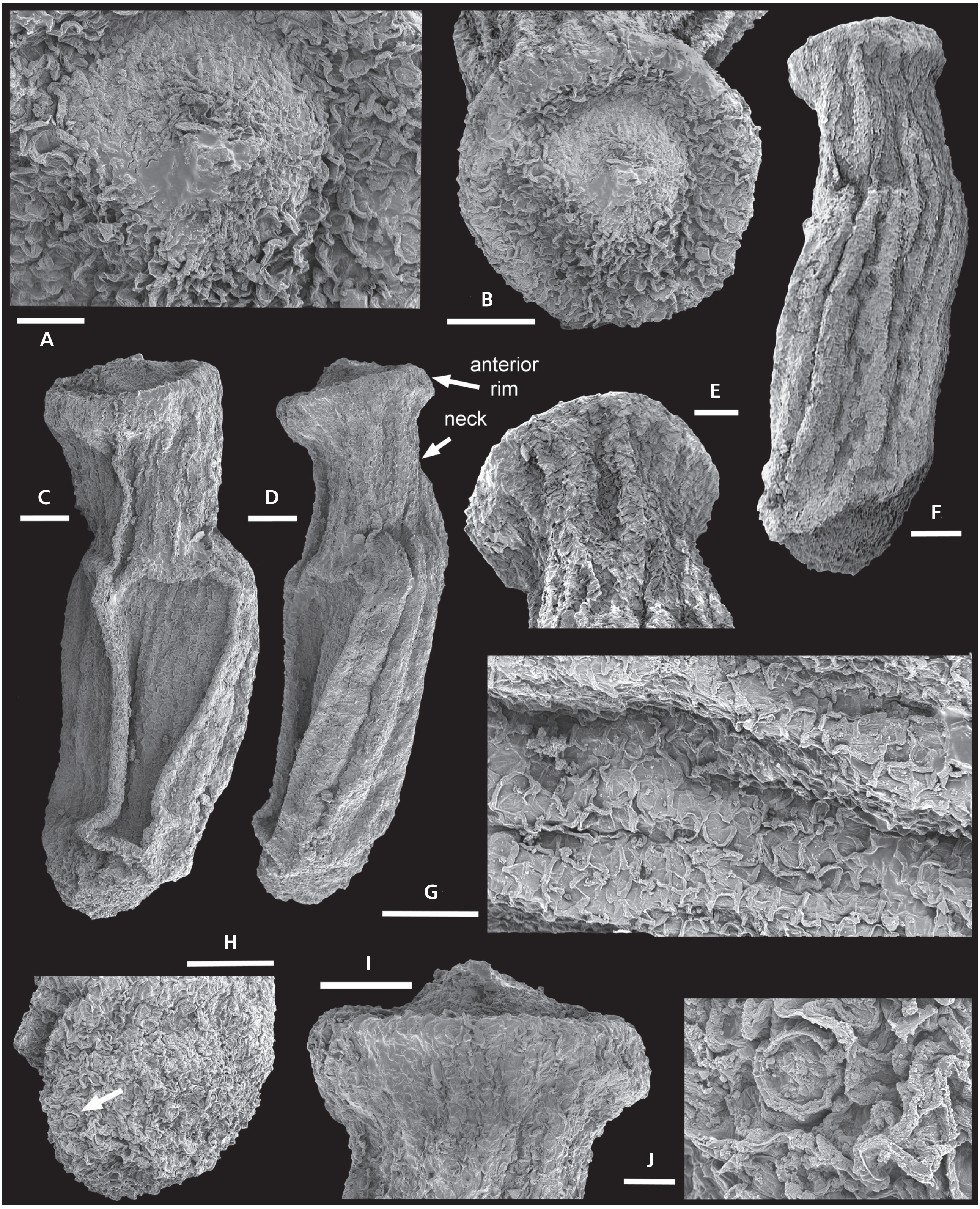

Figure 3. *Inuitiphlaskus kouchinskyi* gen. et sp. nov., hatching larva of total-group priapulid, PMU 28893 from GGU sample 271492, holotype, upper Henson Gletscher Formation, Lauge Koch Land, North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage. A, B – anterior surface with central mound. C, D, F – lateral views. E – oblique view of neck and lower surface of anterior rim. G – detail of surface ornamentation with longitudinal folds oriented horizontally. H, J – circular ridge (arrow in H) possibly representing the attachment of a tubulus or spine. I – lateral view of anterior rim and central mound. Scale bars: 10 µm (J); 40 µm (A, G); 50 µm (E), 100 µm (B–D, F, H, I).

In both species, the introvert may be completely withdrawn (Fig. 1B), as is also considered to be the case in *Inuitiphlaskus kouchinskyi* (Fig. 3). A mouth is not recognised on the anterior surface of *Inuitiphlaskus kouchinskyi* (Fig. 3A, B) but would likely not be visible if the introvert is inverted. In all three taxa, the surface of the trunk is irregularly wrinkled into a crude reticulate pattern. Wennberg *et al.* (2009) illustrated small tubuli developed on the neck of *Priapulus caudatus* and rare circular ridges in *Inuitiphlaskus kouchinskyi* may represent similar structures (Fig. 3H, J).

The central mound on the anterior surface of *Inuitiphlaskus kouchinskyi* (Fig. 3A, B) closely resembles the central mound of *Halicryptus spinosus* (Fig. 1C). Both structures are separated from the apertural rim by a concave area. However, in the illustrated specimen of *Halicryptus spinosus*, the apertural rim carries seven scalids indicating extrusion of the introvert whereas scalids are lacking in *Inuitiphlaskus kouchinskyi* (Fig. 3B, I) and the introvert is considered to be withdrawn.

Discussion

Spherical phosphatised fossils in GGU sample 271492 are similar in diameter (about 400 µm) to the width of *Inuitiphlaskus kouchinskyi*; they may represent eggs of *Inuitiphlaskus kouchinskyi*. The spheres are about five times the diameter (80 µm) of the thousands of eggs produced by *Priapulus caudatus*, the hatching larva of which is substantially smaller than *Inuitiphlaskus kouchinskyi* (Wennberg *et al.* 2009; Fig. 1). However, the few eggs produced by the present day interstitial *Meiopriapulus* attain a diameter of 250 µm (Higgins & Storch 1991) despite the diminutive size of the adult. In the Cambrian literature, such fossil spheres are referred generally to *Olivooides* Qian, 1977 or *Markuelia* Val'kov, 1983. *Olivooides* is interpreted usually as a cnidarian (Dong *et al.* 2016), whereas *Markuelia* is considered to develop into an elongate, worm-like scalidophoran (Dong *et al.* 2010).

The spheres from GGU sample 271492 are similar in size to ovoids interpreted by Yang *et al.* (in press) as eggs within the tube-dwelling stem-group priapulid *Paraselkirkia sinica* Hou, Bergström, Wang, Feng & Chen, 1999 from the Xiaoshiba Lagerstätte (Cambrian Series 2, Stage 3) of South China. Clusters of 3 to 30 ovoid elements (diameter of 300–400 µm) occur within the tubes of individual specimens of *Paraselkirkia sinica* up to 20 mm in length

Stem-group loriciferans were described from the early Cambrian of North Greenland by Peel (2010a, b) and Peel *et al.* (2013) and attain a hundred-fold greater size than their present day meiofaunal relatives in the crown-group. Peel *et al.* (2013, fig. 8) described an urn-shaped post-larva of *Sirilorica carlsbergi* Peel, 2010a, but this preserves a lorica with well-developed plication and its width of almost 20 mm is substantially greater than the 400 µm of *Inuitiphlaskus kouchinskyi*. The enormous reduction in size between the Cambrian *Sirilorica* and present day loriciferan post-larvae supports the notion based on morphological complexity that loriciferan evolution is characterised by an overall developmental miniaturisation (Kristensen 1991a, b). However, Harvey & Butterfield (2017) described specimens of *Eolorica deadwoodensis* Harvey & Butterfield, 2017 from the Deadwood Formation of Canada as a total-group loriciferan in which the overall length was only 300 µm. Harvey & Butterfield (2017) considered that *Eolorica* documented entry of loriciferans into the meiofauna already in late Cambrian (Furongian Series) but accepted their derivation from macromorphic ancestors. While the reduction in size from the hatching larva of *Inuitiphlaskus kouchinskyi* to that of *Priapulus caudatus* and *Halicryptus spinulosus* is much less than that witnessed between *Sirilorica* and present day loriciferans (or *Eolorica*), it may reflect a similar trend in the development of the larval stages of priapulidiform cycloneuralians since the Cambrian, although not in the overall size range of the mature animals themselves.

The limited available morphological information concerning *Inuitiphlaskus kouchinskyi* adds little to our understanding of the overall phylogeny of cycloneuralians. The pattern of early larval development employed by *Inuitiphlaskus kouchinskyi* increases the diversity of developmental strategies of Cambrian cycloneuralians otherwise known from loricate larvae and direct developing worm-like forms such as *Markuelia*, but also in the present day minute interstitial *Meiopriapulus* (Higgins & Storch, 1991). In terms of priapulid evolution, the hatching larva of *Inuitiphlaskus kouchinskyi* indicates a developmental stage that has persisted from the Cambrian until the present day.

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