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The oldest tongue worm: a stem-group pentastomid arthropod from the early middle Cambrian (Wuliuan Stage) of North Greenland (Laurentia)

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ABSTRACT

Rare phosphatised fragments within small shelly fossil assemblages from the upper Henson Gletscher Formation (Cambrian, Miaolingian Series, Wuliuan Stage) of North Greenland (Laurentia) are described as *Dietericambria hensoniensis* n. gen. n. sp. Two pairs of minute cephalic limbs promote comparison with stem-group pentastomids, best known from the late Cambrian (Furongian) Orsten Lagerstätten of Sweden. The North Greenland occurrence is interpreted as the oldest yet described tongue worm and extends the record of pentastomids by about 15 m.y. *Dietericambria hensoniensis* preserves a unique median axial complex of uncertain function, probably an attachment organ; a mouth has not been identified. Isolated hooks and spicules in the samples from the Henson Gletscher Formation are compared to the grasping hooks and copulatory spicules of the extant pentastomid *Raillietiella*, although their interpretation is speculative.

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Stem-group pentastomid; arthropod; Cambrian; Miaolingian; Wuliuan; North Greenland; Laurentia

Present-day pentastomids are annulated, vermiform arthropods commonly known as tongue worms (Riley 1986; Christoffersen & De Assis 2013, 2015). Two pairs of cephalic hooks disposed around the mouth facilitate attachment of the parasites to the soft internal tissues of their host, typically the respiratory tracts of tetrapods, but also in some fishes and insects (Christoffersen & De Assis 2013, 2015). Stem-group pentastomids are particularly well known from the late Cambrian Orsten Lagerstätten of Sweden (Waloszek & Müller 1994; Waloszek et al. 2006; Castellani et al. 2011) but they are also reported from Newfoundland (Waloszek et al. 1994) and the Silurian of the UK (Siveter et al. 2015). The exceptional, early diagenetic phosphatisation through delicate external encrustation of organisms within the Orsten occurrences (Maas et al. 2006) preserves morphologies dissimilar from extant groups, although the diagnostic two pairs of cephalic limbs are well displayed (Fig. 1). Most of the fossil species have few trunk segments and a proportionately large head greater in width than the trunk, although body proportions in *Aengapentastomum* Waloszek, Repetski & Maas, 2006 (Fig. 1C) are more similar to extant forms. Waloszek & Müller (1994) recognised two groups. Members of the “hammer-head” group have greatly enlarged cephalic limbs and include *Heymonsicambria* Waloszek & Müller, 1994 (Fig. 1A). *Boeckelericambria* Waloszek & Müller, 1994 is a “round-head” form (Fig. 1B). While some extant pentastomatids may attain a length of about 160 mm, known Orsten specimens rarely exceed a length of 1–2 mm. They have been interpreted as larvae within the meiofauna (Waloszek & Müller 1994; Maas et al. 2006; Christoffersen & De Assis 2015), or even micromorphic adults (Sanders & Lee

2010), but their small size may also reflect preservational size limits imposed by the phosphatisation process.

This paper describes rare vermiform fossils from the middle Cambrian (Miaolingian Series, Wuliuan Stage) Henson Gletscher Formation of North Greenland (Fig. 2). They are interpreted as the oldest described stem-group pentastomids, some 15 m.y. older than records from the late Furongian Orsten of Sweden. The fragmentary remains are phosphatised, although their preservation is much coarser than the exquisitely preserved Orsten material. Interpretation as a stem-group pentastomid reflects general form and the identification of two pairs of minute cephalic limbs in the holotype of the type species, *Dietericambria hensoniensis* n. gen. n. sp. (Fig. 3), although these are much smaller than the cephalic limbs seen in Orsten species (Fig. 1). The median axial area of the head of *Dietericambria hensoniensis* also retains a complex of flange-like structures of uncertain function without equivalence in Orsten forms. Detached hooks and spicules from the same Greenland samples are compared to similar sclerotised structures in extant pentastomids, but direct evidence of their association with *Dietericambria hensoniensis* is lacking.

Background

The Henson Gletscher Formation in the western Peary Land to Lauge Koch Land region (Fig. 2) is a constituent formation of a prograding complex of Cambrian–early Ordovician shelf carbonates and siliciclastic sediments, referred to the Brønlund Fjord and Tavsens Iskappe groups (Higgins et al. 1991; Ineson & Peel 1997; Geyer & Peel 2011; Peel et al. 2016; Peel &

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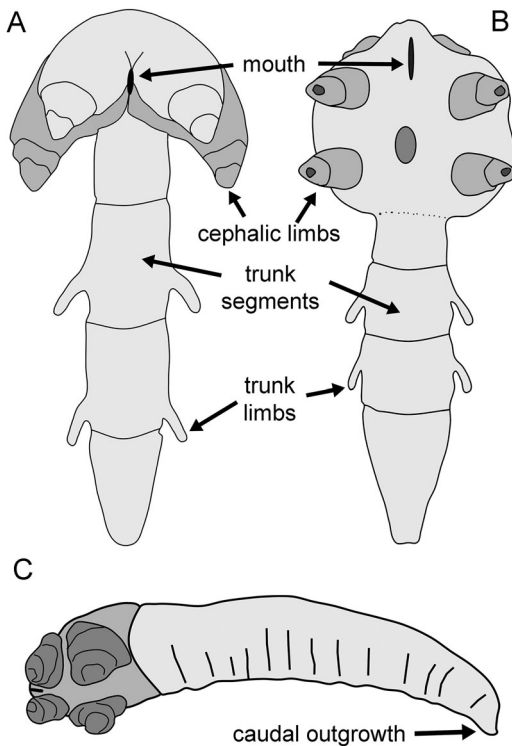


Figure 1. Cambrian stem-group pentastomids from Sweden. **A.** *Heymsonicambria* Waloszek & Müller, 1994, a “hammer-head” stem-group pentastomid. **B.** *Boeckericambria* Waloszek & Müller, 1994, a “round-head” stem-group pentastomid. **C.** *Aengapentastomum* Waloszek, Repetski & Maas, 2006. Schematic sketches redrawn after Waloszek & Müller (1994, fig. 1), Castellani et al. (2011, text-fig. 1) and Waloszek et al (2006, fig. 3).

Kouchinsky 2022). The highly fossiliferous formation is composed mainly of dark, recessive, limestones, dolostones and mudstones, but a middle member consists of pale fine-grained sandstones.

Fossil assemblages from the Henson Gletscher Formation in southern Lauge Koch Land and Løndal range in age from Cambrian Series 2 (Stage 4) to the Miaolingian Series (Wuliuan Stage; *Ptychagnostus gibbus* Biozone), but Drumian Stage strata occur to the west in outcrops along the northern coast of North Greenland (Higgins et al. 1991; Robison 1994; Blaker & Peel 1997; Ineson & Peel 1997; Geyer & Peel 2011). Trilobite assemblages from the Henson Gletscher Formation have a Laurentian

aspect but include species, associated with agnostoids, that are important for international correlation with Siberia, the Altai Sayan fold belt and South China (Blaker & Peel 1997; Geyer & Peel 2011). Additional faunal elements have been described by Clausen & Peel (2012), Peel (2015, 2017, 2019, 2021), Peel et al. (2016) and Peel & Kouchinsky (2022).

Material

Grønlands Geologiske Undersøgelse (GGU) samples 218831 and 271492 were collected at 56.5 m above the base of the Henson Gletscher Formation at its type locality in Lauge Koch Land, where the formation attains a thickness of 62 m, in scours on the top of a 1-m-thick mass flow deposit (82°10'N, 40°24'W; Ineson & Peel 1997, fig. 31; Geyer & Peel 2011, fig. 3; Fig. 1A). GGU sample 218831 (weight about 200 g) was collected by Peter Frykman on 24th June 1979. GGU sample 271492 (weight about 2 kg) was collected by J.S. Peel on 25th June 1978.

GGU sample 271718 (weight about 5 kg) was collected by J.S. Peel on 15th July 1978 from a thin-bedded, phosphatised, dark dolomitic limestone occurring about 1 m below the top of the formation on the west side of Løndal (82°18'N, 37°03'W; Clausen & Peel 2012, fig. 1; Fig. 1C), where the formation has thinned to 47 m.

Specimens were hand picked from residues of limestone dissolved in 10% acetic acid, prior to examination and imaging by scanning electron microscopy. Images were assembled in Adobe Photoshop CS4.

Abbreviations and repositories

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

STEM-GROUP PENTASTOMIDS Genus *Dietericambria* new genus

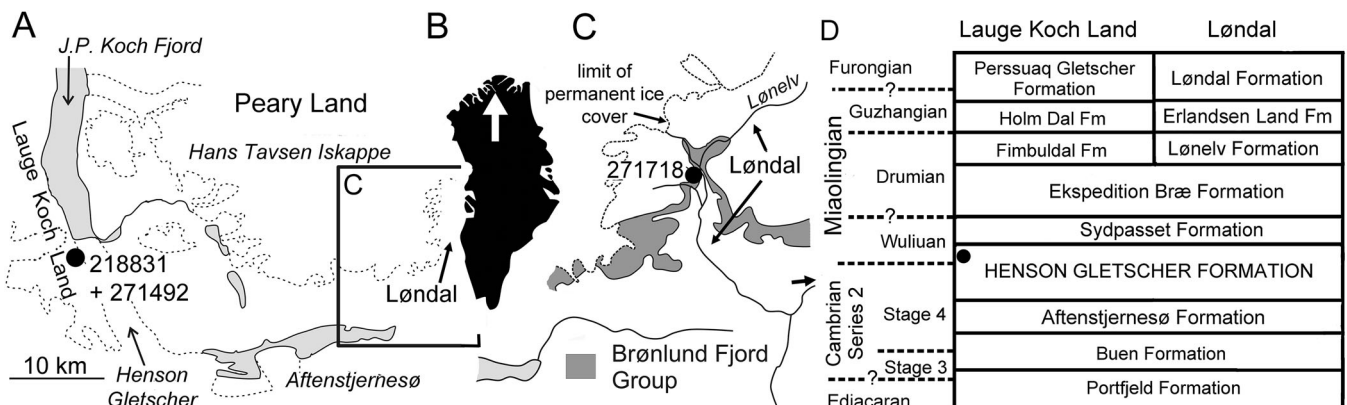


Figure 2. Geographical and geological background. **A.** Location of GGU samples 218831 and 271492 in southern Lauge Koch Land with inset of **C.** **B.** Greenland showing location (arrow) of J.P. Koch Fjord. **C.** Løndal region of western Peary Land showing the location of GGU sample 271718. **D.** Cambrian stratigraphy showing the location of GGU samples in the Henson Gletscher Formation (black dot).

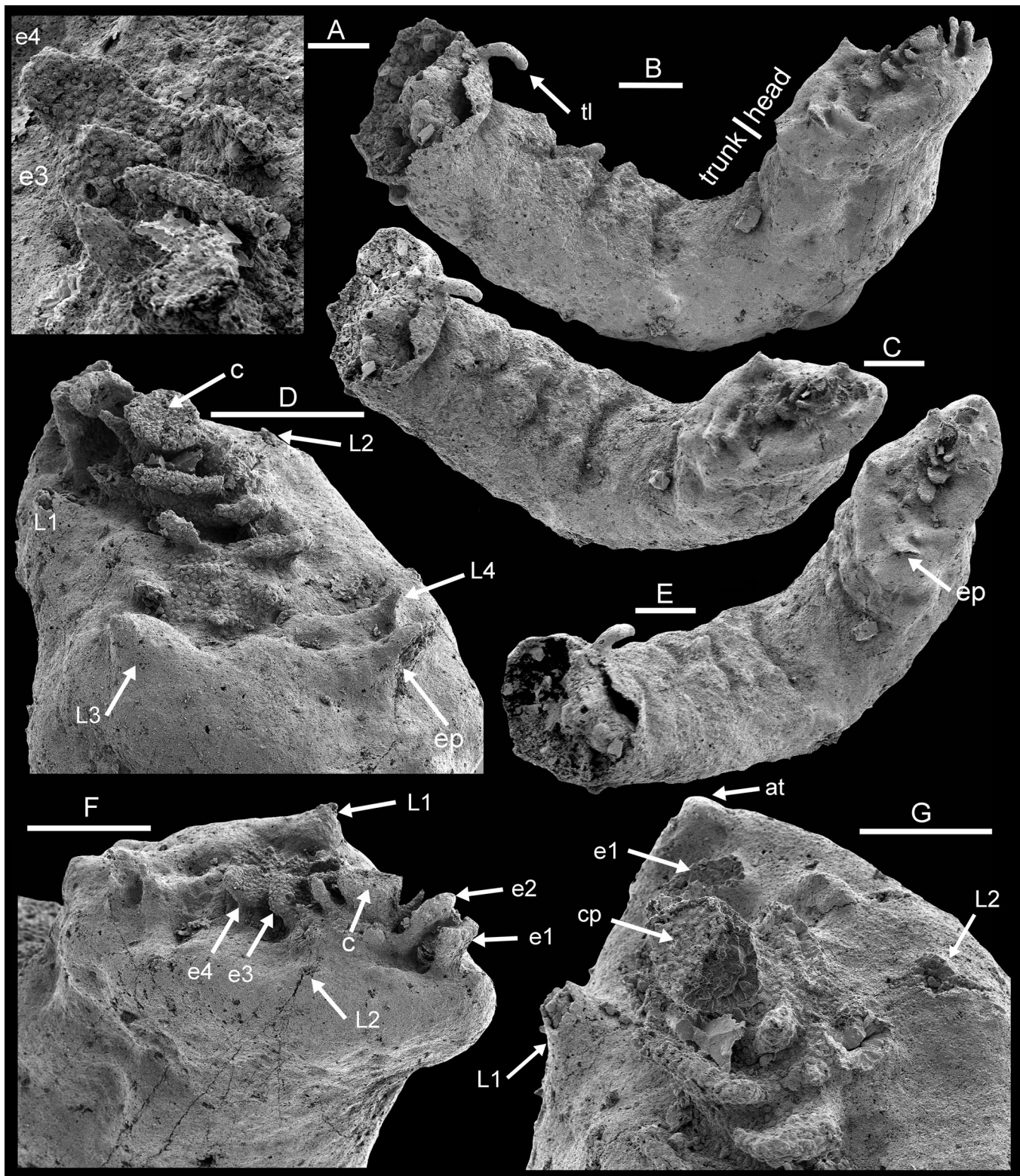


Figure 3. *Dietericambria hensoniensis* n. gen. n. sp., PMU 39167 from GGU sample 271492, holotype, Henson Gletscher Formation, southern Lauge Koch Land, Cambrian (Miaolingian Series, Wuliuan Stage). **A.** Detail of Fig. 4C showing ornamentation of median axial complex on ventral surface of head. **B,C,E.** Oblique lateral and ventro-lateral views of head and trunk. **D,F,G.** Oblique ventral (**D,G**) and oblique lateral (**F**) of head. Abbreviations: at, anterior tubercle; c, central raised disc; cp, papillate surface of central raised disc; e1–e4, flange-like extensions; ep, posterior flange-like extension; L1–L4, cephalic limbs; tl, trunk limb. Scale bars: 20 µm (A), 50 µm (G), 100 µm (B–F).

Type species. – *Dietericambria hensoniensis* n. gen. n. sp. from the Henson Gletscher Formation of North Greenland; Cambrian, Miaolingian Series, Wuliuan Stage.

Diagnosis. – An elongate pentastomid with a complex of steeply inclined flanges in the median axial region of the head. Head oval, of similar width to the trunk, with four minute

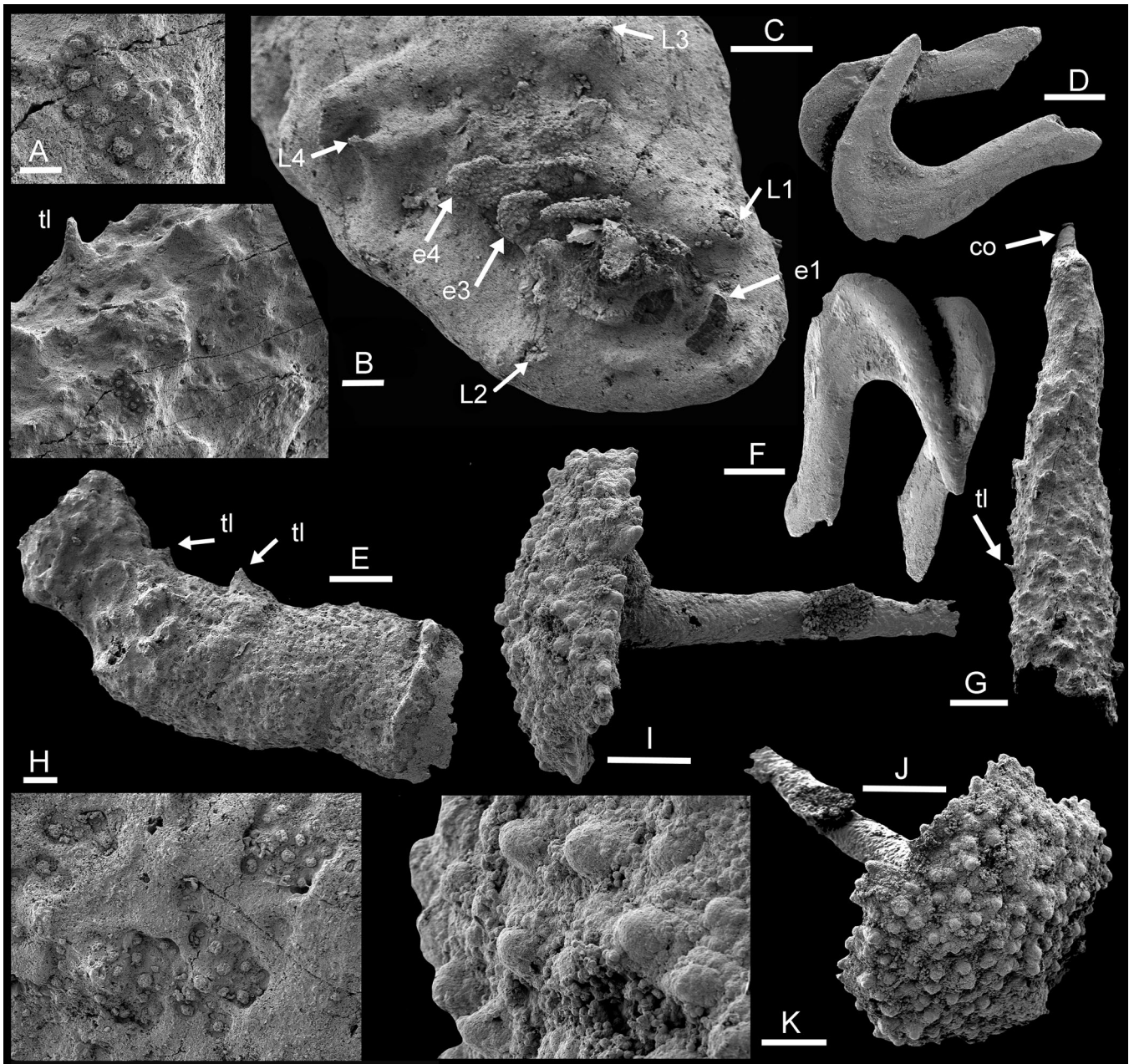


Figure 4. A–C,E,G,H. *Dietericambria hensoniensis* n. gen. n. sp., Henson Gletscher Formation. Cambrian (Miaolingian Series, Wuliuan Stage). A,B,G. PMU 36169 from GGU sample 271718, Løndal, posterior, with caudal outgrowth (co), trunk limb or spine (tl) and patches of ornamentation beneath phosphatic encrustation. C. PMU 39167 from GGU sample 271492, holotype, head, abbreviations see Fig. 3. E,H. PMU 39168 from GGU sample 271492, fragment of trunk with trunk limbs or spines (tl) and detail of sculpture (H). D,F. Conjoined pair of opposing hooks resembling eupentastomid cephalic hooks. PMU 36170 from GGU 218831. I–K. Spicule with ornamented base, PMU 36171 from GGU sample 271492. Scale bars: 5 µm (H), 10 µm (A,K), 30 µm (B), 50 µm (C,I,J), 100 µm (D–G).

limbs; trunk with six or more segments and small trunk limbs. Posterior without apparent annulation; tapering to a short caudal outgrowth.

Etymology. – For Dieter Waloszek in recognition of his studies of Swedish Orsten fossils, including stem-group pentastomids.

Discussion. – *Dietericambria* is readily distinguished from described “hammer-head” and “round-head” Cambrian stem-group pentastomids (Fig. 1) by its narrow oval head with minute limbs, greater number of trunk segments, extended posterior section and the complex of steeply inclined

flanges in the median axial region of the head (Fig. 3). *Aengapentastomum andresi* Waloszek, Repetski & Maas, 2006 from the lower Ordovician (Tremadoc) of Västergötland, Sweden (but likely reworked from underlying late Cambrian according to Waloszek et al. 2006), has a similar elongate annulated form to *Dietericambria* but with more prominent, robust, cephalic limbs. Additionally, *Aengapentastomum andresi* lacks the median axial complex of flanges that characterises the head of *Dietericambria*.

Dietericambria hensoniensis n. gen. n. sp.
Figures 3, 4A–C,E,G,H

Holotype – PMU 39167 from GGU sample 271492, Henson Gletscher Formation, southern Lauge Koch Land, North Greenland. Cambrian, Miaolingian Series, Wuliuan Stage.

Other figured material. – PMU 39168, a section of the trunk from GGU sample 271492, southern Lauge Koch Land; PMU 39169, a posterior fragment from GGU sample 271718, Løndal, Peary Land. All specimens from the Henson Gletscher Formation; Cambrian, Miaolingian Series, Wuliuan Stage. A pair of conjoined hooks from GGU sample 218831 (PMU 36170; Fig. 4D and F) and a sclerite from GGU sample 271492 (PMU 36171; Fig. 4I–K) are discussed below.

Etymology. – From its occurrence in the type section of the Henson Gletscher Formation, southern Lauge Koch Land, adjacent to Henson Gletscher (Fig. 2).

Description. – The holotype is an incomplete specimen about 1.2 mm long, preserving the head and the thorax; the posterior extremity is broken (Fig. 3B,C,E). It is cylindrical in form, with a maximum diameter of about 270 µm, and curved along its length such that the ventral surface is well displayed along the inside of the curve. The head has a length of 350 µm, with convex sides narrowing forward to meet at the pointed anterior end (Fig. 3E, G). It is shallowly convex but the posterior margin is upturned; its maximum width lies near to the posterior margin, which is shallowly convex in plan view. The thorax consists of at least six fused segments or annulations that are delimited on the ventral surface by broad grooves, but obscure on the lateral and dorsal surfaces. The margins of the segments on the ventral surface are raised, with conical tubercles present ventrally (Fig. 3C). A trunk limb extends from the final preserved segment (Fig. 3B, arrow tl) and it is likely that similar limbs or spines arose from the conical tubercles. The ventral surface of the trunk is covered by closely spaced, circular papillae, which pass gradually into smooth lateral areas (Fig. 3B). At its broken posterior margin, the outer surface of the trunk is seen to be preserved as a compact layer overlying coarse, granular and crystalline phosphatised fill of the inner cavity (Fig. 3B,C,E).

The ventral surface of the head preserves a complex array of structures, with smooth peripheral areas surrounding an axial zone ornamented by round papillae 1–2 µm in diameter (Fig. 3A,D; Fig. 4C). The papillate zone grades into the surrounding smooth areas, which display a uniform texture on the ventral surface. In the broken, smooth, conical protruberances, which are interpreted as minute cephalic limbs (Fig. 3D,G and Fig. 4C, arrows L1 and L2), the outer surface is seen to be a thin brittle layer about 1 µm in thickness and overlying an inner granular core. The anterior terminates in a small conical tubercle (Fig. 3G, arrow at). Four small conical cephalic limbs (L1–L4) are recognised but display no preserved traces of segmentation or terminal hooks (Fig. 3D,G and Fig. 4C). The median papillated complex appears to be formed of a series of steeply inclined, flange-like extensions of the ventral surface (Fig. 3F, arrows e1–e4) located mainly anterior (e1 and e2) or posterior (e3 and e4) of a central raised disc (c; Fig. 3D,F,G and Fig. 4C). The rounded edges of these flanges locally appear to be cylinders or tubes (Fig. 3A,D). An

additional, partially broken extension (Fig. 3D,E, arrow ep) lies posterior to limbs L3 and L4 but closer to L4.

A second specimen consists of a fragment of the trunk with conical bases of the trunk limbs or spines (Fig. 4E, arrows tl). It is broken at the anterior and posterior ends, but a transverse ridge at the anterior end may represent the posterior margin of the head. Most of the surface is covered with diagenetic encrustation but the characteristic papillate ornamentation of small circular tubercles is visible in patches (Fig. 4H). The posterior section is narrower and appears to lack segmentation. In this respect, it is comparable to a third specimen (Fig. 4G) that seems to have a crude honeycomb pattern of ridges, with raised tubercles and short spines but without annulations (Fig. 4B,G, arrow tl). This fragment displays similar papillate ornamentation to other specimens beneath the diagenetic encrustation (Fig. 4A,B) and tapers posteriorly towards a small caudal outgrowth (Fig. 4G, arrow co).

Discussion. – In terms of its overall slender shape, tapering towards the posterior, *Dietericambria hensoniensis* most closely resembles the late Furongian–?early Ordovician *Aengapentastomum andresi* amongst described stem-group pentastomids (Andres 1989; Waloszek & Müller 1994; Waloszek et al. 1994, 2006; Castellani et al. 2011). However, *Dietericambria hensoniensis* is distinguished by its much smaller cephalic limbs, which lack segmentation, and the presence of the median axial cephalic complex.

At first glance, some elements of the median axial cephalic complex on the ventral surface of the head appear to be limbs, but closer examination indicates that these elongate rounded surfaces represent the peripheral margins of flanges. In lateral view (Fig. 3F), individual flanges are seen to slope steeply in towards the flat-topped, circular pillar (c). The presence of the same papillate ornamentation of closely spaced, flat-topped tubercles (Fig. 3A) that is seen on the trunk of all three illustrated specimens confirms that the preserved surface of the cephalic flanges is the external surface of the integument and not a mould of its interior. Similar papillation is seen in *Heymonsicambria* from Västergötland, Sweden, illustrated by Castellani et al. (2011, fig. 9), but on the caudal outgrowth. Equally, the distribution of similar papillae on the trunk of *Dietericambria hensoniensis* (Fig. 4A,H) indicates that the ornamentation of the median axial cephalic complex is not an impression of a surface to which the head may have been attached.

The position of the mouth has not been located in *Dietericambria hensoniensis*. The mouth in *Boeckelericambria* and *Aengapentastomum* is located forward of the anterior pair of cephalic limbs, while it is located between the inflated basal segments of the anterior limbs in *Heymonsicambria* (Waloszek & Müller 1994; Waloszek et al. 1994; Castellani et al. 2011; Fig. 1). The symmetry of the flanges of the median axial complex might suggest that the circular central pillar (Fig. 3F, arrow c) represented a protruding mouth, but the undamaged part of the flat surface of the structure preserves the external integumental papillation (Fig. 3G, arrow cp).

Trunk limbs in Orsten pentastomids (Waloszek & Müller 1994; Fig. 1A,B) are minute structures located on the lateral surfaces in contrast to the ventrally located limbs of *Dietericambria hensoniensis* (Fig. 3C). In this respect, limb placement

in the latter more closely resembles that seen in many tardigrades (Nelson et al. 2015; Gross et al. 2017). However, the much more robust limbs in the minute stem-group tardigrade from the Miaolingian of Siberia described by Müller et al. (1995) are also disposed laterally (Waloszek et al. 2003; Maas et al. 2006).

Cambrian pentastomid hooks

Two opposing but diagenetically conjoined hooks from GGU sample 218831 (Fig. 4D,F) invite comparison with the cephalic hooks of eupentastomids, the present-day Pentastomatida (Fig. 5; Christopher & De Assis 2015). Hooks are also present as claws at the termination of tardigrade limbs (Nelson et al. 2015, fig. 17.8) but generally lack the rounded V-shape with a broader basal shaft and a narrower, tapering barb seen in the Henson Gletscher specimens (for terminology see Fig. 5C). The length of the hooks from the Henson Gletscher Formation, measured along the basal shaft, approaches 500 µm. The hooks are shallowly convex on one side in cross-section (top surface of uppermost hook in Fig. 4D,F), but flattened with an acute margin on the other (upper surface of lower hook). The cross-section thickens as the culmination of the V-shape is approached, with an extension into a thin sheet within the angle of the culmination of the V-shape. The basal termination is broken in both specimens but the tip of the barb is acutely rounded. The hooks are juxtaposed so

that the flattened surfaces are in proximity to each other, and likely facing each other in life. As oriented (Fig. 4D), the uppermost hook would lie on the right side of the head, with the lower hook on the left side if the interpretation as cephalic hooks is correct.

Cephalic hooks in extant pentastomids are heavily sclerotised and widely used in delimiting species (Riley 1986; Christoffersen & De Assis 2013, 2015). The disposition of cephalic hooks in *Raillietiella* Sambon, 1910, the most diverse genus of Protostomida in terms of number of described species, was illustrated by Kelehear et al. (2011, fig. 2) who noted that the sharpness of the tip of the barb was related to the body size of the animal. Two pairs of cephalic hooks are present in *Raillietiella*, although males also develop a pair of copulatory spicules (Fig. 5A).

There is no conclusive evidence to indicate that the described, supposed cephalic hooks from the Henson Gletscher Formation belonged to *Dietericambria hensoniensis*. Indeed, the length of each hook (500 µm) greatly exceeds the width of the head (about 270 µm) in the holotype. However, the ontogenetic size range and stage in ontogenetic development of *Dietericambria hensoniensis* are not known. The three available fragments of *Dietericambria hensoniensis* are of similar size, but this may reflect diagenetic bias, post-mortem sorting or ecological separation rather than just a similar ontogenetic stage. Maas et al. (2006) considered that a large part of the Orsten assemblages of Sweden had

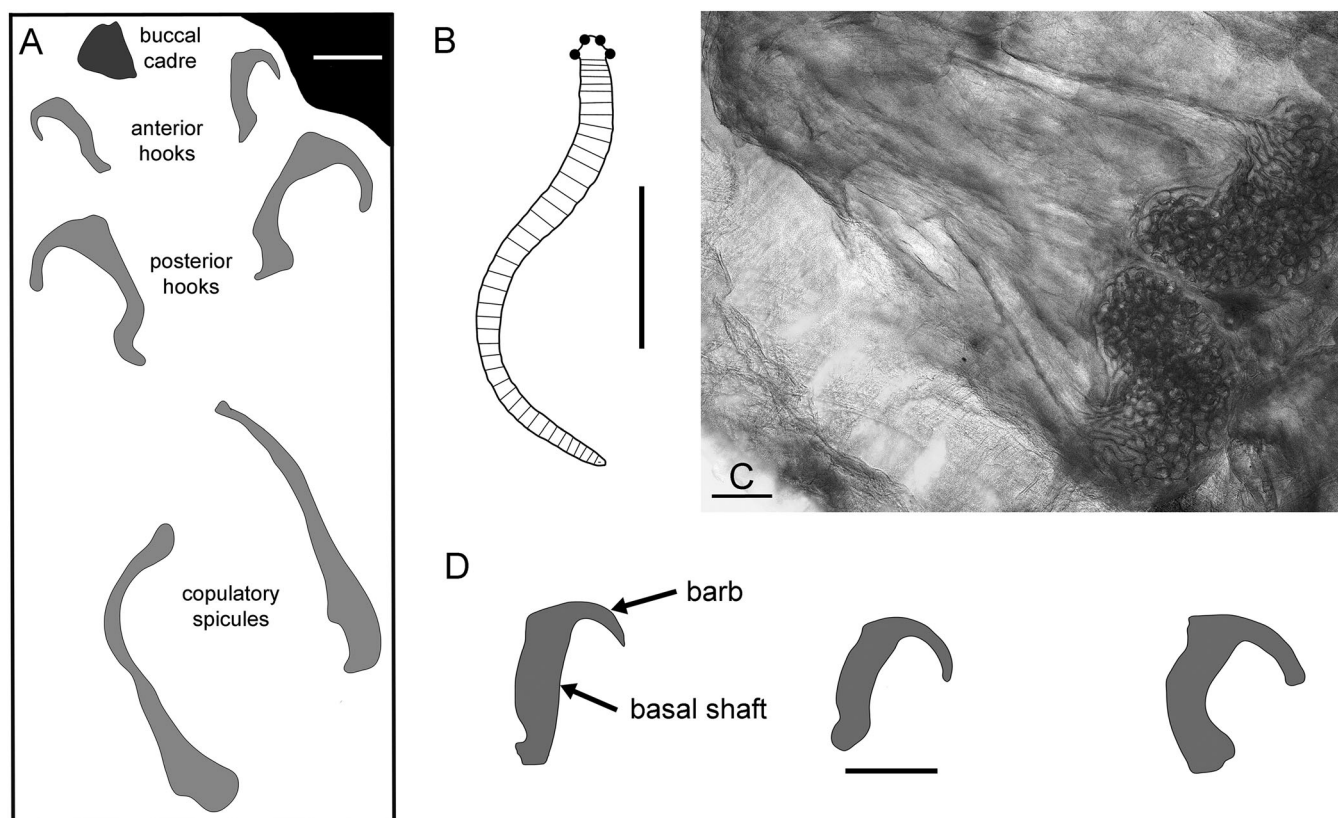


Figure 5. Cephalic hooks and copulatory spicules of the extant pentastomid (Eupentastomida) *Raillietiella* Sambon, 1910. **A.** Sketch of anterior of male *Raillietiella frenatus* Ali, Riley & Self, 1981 showing cephalic hooks and copulatory spicules (drawn from Kelehear et al. 2011, fig. 2b). **B.** Female with cephalic hooks (black dots on head) and multi-annulated trunk (drawn from Riley 1986, fig. 2a). **C.** Copulatory spicules of male *Raillietiella orientalis* (Hett, 1915) (copyright Crystal Kelehear; reproduced from Kelehear et al. 2011, fig. 4c). **D.** Cephalic hooks of *Raillietiella frenatus* showing size-related transition from pointed to blunt hooks (drawn from Kelehear et al. 2011, fig. 3). Scale bars: 100 µm (A,C,D); 10 mm (B).

a meiofaunal origin. Other phosphatised small shelly fossils from within the samples from the Henson Gletscher Formation tend to have a similar size range and the GGU samples represent re-deposited sediments in a background of fine argillaceous deposits. Larger specimens of several constituent taxa from the small shelly fossil assemblage are known from unprocessed rock surfaces but are generally not phosphatised.

Waloszek & Müller (1994) and Castellani et al. (2011) considered the most distal part of the segmented cephalic limbs in described Cambrian stem-group pentastomids to be a finger-like claw. Hooks of the type described herein (Fig. 4D,F) have not been described previously in fossil material, although they are present in extant pentastomids (Fig. 5).

Extant males of the pentastomid *Raillietiella* develop copulatory spicules that are club-shaped rather than V-shaped (Fig. 5A). In some species the base of these spicules may be extended into a platform, the lower surface of which is covered with a prominent raised ornamentation (Riley 1986, fig. 5d; Kelehear et al. 2011, fig. 4c; Fig. 5C). Rare spicules of similar form are present in GGU sample 271492 (Fig. 4I–K), although their assignment to pentastomids and interpretation as copulatory spicules is speculative.

Mode of life

Present-day eupentastomids generally have a complex developmental cycle associated with their internal parasitic habit, mainly in tetrapods, birds and fishes, but they can occur in humans (Riley 1986; Christoffersen & De Assis 2013, 2015; Tappe & Büttner 2009; Klompmaker & Boxhall 2015). Insects may be important intermediary hosts (Galecki & Sokół 2019). None of these host groups occur in the Cambrian but it has been suggested that stem-group pentastomids may have been associated with marine conodont-bearing vertebrates at that time (Sanders & Lee 2010; Klompmaker & Boxhall 2015). Conodont sclerites are often conspicuous in Cambrian samples, including those examined here. Many of the hosts are terrestrial, unlike the marine stem-group species, but eupentastomids occur in both marine and freshwater fishes. Numerous large arthropods and other invertebrate groups that lived in Cambrian seas might have been hosts to pentastomids. In the early Cambrian of North Greenland, specimens of poorly sclerotised lobopodians attain a length of more than 40 cm, while co-occurring arthropods may be half this size (Budd 1998; Peel & Ineson 2011; Stein et al. 2013; Harper et al. 2019). However, direct fossil evidence of such associations is lacking. A Silurian pentastomid from the UK was described as a parasite associated with an ostracod by Siveter et al. (2015), although De Baets & Littlewood (2015) considered this to be ectoparasitic rather than endoparasitic. The cephalic limbs and median axial complex of *Dietericambria hensoniensis* support interpretation as a parasite, but the host is unknown. Neither is it not known if it was attached to the exterior or interior of its host. External attachment may also represent symbiosis, as is the case with tiny worms attached to the exterior of early Cambrian palaeoscolecids from China described by Cong et al. (2017). However, Zhang et al. (2020) considered encrustations of tubes on the exterior of

Cambrian (Stage 4) brachiopods from South China to represent kleptoparasitism. Traces of parasitism or other forms of commensalism may be recorded also in the shells of invertebrates without clear evidence of their perpetrator (Peel 2014).

On account of morphological similarities, stem-group pentastomids have been interpreted generally as larvae, although Sanders & Lee (2010) questioned this interpretation. While interpreted as meiofauna (Waloszek & Müller 1994; Maas et al. 2006; Christoffersen & De Assis 2015), their occurrence together with small shelly fossils of similar size in the assemblages from the Henson Gletscher Formation suggests a strong environmental or taphonomic influence on diagenetic phosphatisation. Other species present in the microfossil residues are usually not phosphatised when preserved as macrofossils in hand specimens.

Evolution

Waloszek et al. (2006) established the crown-group Eupentastomida Waloszek, Repetski & Maas, 2006 to include present day pentastomids, placing the Cambrian Orsten fossils (Andres 1989; Waloszek & Müller 1994; Waloszek et al. 1994, 2006; Castellani et al. 2011) within the pentastomid stem. They concluded that the systematic position of Pentastomida was unresolved, but stressed the fundamental role of morphological data in establishing the ground patterns of evolution. While accepting that many morphological features were arthropodan, they excluded pentastomids from Arthropoda *sensu stricta*, in the sense of Maas et al. (2004). Sanders & Lee (2010) suggested that the appearance of late Cambrian parasitic pentastomids so soon after that of the first early Cambrian crustaceans contradicted the hypothesis that pentastomids are allied to advanced crustaceans, which may add support for the interpretation of stem-group pentastomids as offshoots of early arthropods (Castellani et al. 2011). This argument is strengthened by the present extension of the range of stem-group pentastomids by some 15 m.y., back to the early middle Cambrian Wuliuan Stage. However, Sanders & Lee (2010) presented estimated molecular dates for the origin of pentastomids of 490–520 m.y., which encompasses the upper three series of the Cambrian, and proposed a close relationship to branchiurans.

Molecular data presented by Oakley et al. (2013) and others placed present-day pentastomids within the sclerotised arthropods, as eucrustacean euarthropods (Klompmaker & Boxhall 2015; Giribet & Edgecombe 2019). Wheat & Wahlberg (2013) followed Sanders & Lee (2010) and suggested that Cambrian–Ordovician stem-group pentastomids may represent a stem group of the common ancestor of branchiurans and pentastomids, but this conflicts with the interpretation of Cambrian species as stem-group pentastomids. Christoffersen & De Assis (2013, 2015) gave extensive reviews of the history of pentastomid research and recognised a Phylum Pentastomida Huxley, 1869 (Pan-Pentastomida of Almeida & Christoffersen 1999) that included the Palaeozoic stem-group species together with present-day taxa placed within the crown-group Eupentastomida.

Haug et al. (2021) reviewed the literature based on molecular and morphological data that suggested that eupentastomids

are crustaceans. They urged caution in accepting this interpretation due to the absence of morphological features of crustaceans, while accepting that this might result from modification due to the parasitic habit. As regards the stem-group pentastomids, Haug et al. (2021) noted that some showed an astonishing degree of morphological similarity to extant pentastomids, which De Baets et al. (2021) suggested provided unambiguous evidence of parasitism.

Specimens of *Dietericambria hensoniensis* (Figs 3, 4) from the Henson Gletscher Formation of North Greenland are interpreted as the oldest described stem-group pentastomids. They were collected from the early middle Cambrian (Wuliuan Stage of the Miaolingian Series) and are thus almost 15 m.y. older than stem-group pentastomids described from the late Cambrian (late Furongian Series) by Waloszek & Müller (1994), Waloszek et al. (2006) and Castellani et al. (2011). From an evolutionary perspective, the age difference may explain the minute (incipient?) size of the cephalic limbs of *Dietericambria hensoniensis* when compared to those of the “hammer-head” and “round-head” groups of stem-group pentastomids described by Waloszek & Müller (1994). Furthermore, the median axial complex of flanges in the head of *Dietericambria hensoniensis*, which is assumed to be related to the mouth, is not present in the younger forms, where the mouth is usually a simple slit. It likely represents an attachment structure associated with the mouth. Together with the minute cephalic limbs, it may represent an evolutionary stage prior to the development in later stem-group pentastomids (the Orsten pentastomids) of enlarged cephalic limbs with claws or hooks for attachment to the host and a simplified mouth.

Rare hooks (Fig. 4D,F) and spicules (Fig. 4I,J) from the Henson Gletscher Formation closely resemble cephalic hooks and copulatory spicules occurring in the extant eupentastomid *Raillietiella*. If correctly identified, they represent the oldest known occurrences of such structures, although no direct association with *Raillietiella* is implied. Neither is there direct evidence of the association of the hooks and spines with *Dietericambria hensoniensis*, although their size indicates that they would have been associated with much larger individuals than those currently available.

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Disclosure statement

No potential conflict of interest was reported by the author(s).

Data archiving statement

This published work and the nomenclatural acts it contains have been registered in Zoobank: zoobank.org/pub:04-D7A5AB-6FD4-42D5-B358-09049D13516F

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