

A possibly deep branching artiopodan arthropod from the lower Cambrian Sirius Passet Lagerstätte (North Greenland)

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Abstract: Artiopoda was a diverse group of Palaeozoic euarthropods that proliferated in the early Palaeozoic, epitomized by the ubiquitous trilobites. Their possible phylogenetic position outside mandibulates and chelicerates offers the potential for understanding the evolution of euarthropods in more detail. However, this opportunity remains unexploited given that identification of deep-splitting artiopodans remains to be fully explored. Here, we describe a new non-trilobite artiopodan from the lower Cambrian Sirius Passet Lagerstätte, North Greenland. *Thulaspis tholops* gen. et sp. nov. is a large species with a broad, domed head shield, followed by a trunk consisting of 15 thoracic tergites and a small pygidium, giving the body an ovoid appearance when viewed dorsally. *Thulaspis* is distinctive with its

rounded genae and anterior thoracic pleural tips, as well as short pleural spines posteriorly. A heart-shaped hypostome with an anterior lobe is present. Appendages, partly obscured by the tergal skeleton, have many moderate length gnathobasic spines, and large flap-like exopods with a fringe of small setae. Cladistic analyses recover *Thulaspis* as the sister taxon to *Squamacula*, a genus found in the Chengjiang and Emu Bay Shale biotas, in either a polytomy with a number of artiopodan taxa or as a sister group to all other artiopodans, indicating an important role in understanding the roots of artiopodan anatomy and evolution.

Key words: Artiopoda, Euarthropoda, Sirius Passet Lagerstätte.

EUARTHROPODA is the most diverse animal phylum today. The group evolved an immense morphological disparity, facilitating a range of feeding strategies and exploitation of multitudes of ecological niches in modern day ecosystems (Ødegaard 2000). Their adaptive body plan gave rise to a rapid diversification during the Cambrian radiation, between Stages 2 and 3 (Edgecombe & Legg 2014; Ortega-Hernández 2016; Daley *et al.* 2018; Edgecombe 2020; Aria 2022). One of these groups, Artiopoda, was an especially diverse euarthropod clade in the Palaeozoic, best known for the biomineralized trilobites (Hou & Bergström 1997). Artiopodans have the potential to recover relationships between euarthropod total-groups but their phylogenetic position is contested (Giribet & Edgecombe 2019; Aria 2022). Artiopoda has been proposed as being part of the mandibulate stem (Scholtz & Edgecombe 2005; Ortega-Hernández *et al.* 2013; Stein *et al.* 2013; Zeng *et al.* 2017, 2020; Aria *et al.* 2020), the chelicerate stem (Legg *et al.* 2013; Vannier *et al.* 2018;

Aria 2020) and the euarthropod stem (Aria & Caron 2017). These studies were based mainly on non-mineralized taxa particularly from Cambrian Lagerstätten (Stein & Selden 2012; Lerosey-Aubril *et al.* 2013a, 2013b, 2017; Ortega-Hernández *et al.* 2013; Stein *et al.* 2013; Du *et al.* 2019) but current data have proved insufficient to reach a consensus. Therefore, descriptions of new taxa, particularly possible deep branches with more plesiomorphic traits, are crucial to resolve this.

There are several major groups in Artiopoda that are usually recovered as clades: Cheloniellida, Conciliterga, Aglaspida, Nektaspida, Xandarella and of course Trilobita (Legg *et al.* 2013; Ortega-Hernández *et al.* 2013). The interrelationships between these groups are less accepted although they repeatedly fall within larger-scale clades, namely Trilobitomorpha and Vicissicaudata (Legg *et al.* 2013; Ortega-Hernández *et al.* 2013). There are a few proposed smaller clades, such as Retificiida and Protosutura, which have limited diversity (two to three genera). While Protosutura is a

fairly recent proposal (Du *et al.* 2019), Retificiida was constructed in 1997 and included its namesake, *Retificies* Hou & Bergström, 1997, as well as *Squamacula* Hou & Bergström, 1997 tentatively. Retificiida has recently been called into question (Zhang *et al.* 2022) because of a lack of support in most analyses for the enigmatic *Squamacula* as a constituent genus. Furthermore, the appendicular morphology of these taxa has been shown to differ greatly (Zhang *et al.* 2004, 2022). However, a close relationship has been consistently recovered between *Pygmaclypeatus* Zhang *et al.*, 2000 and *Retificies*, and is well supported now that their appendicular morphologies are well understood (Schmidt *et al.* 2022; Zhang *et al.* 2022). Several other taxa such as *Squamacula*, *Sidneyia* Walcott, 1911 and *Emeraldella* Walcott, 1912 are usually recovered as early members of large-scale clades such as Trilobitomorpha and Vicissicaudata or, in the case of *Squamacula*, of Artiopoda, but their exact position remains fluid depending on the dataset. Protosutura, Retificiida and these enigmatic taxa are often positioned deep in the tree with either Retificiida or *Squamacula* usually positioned as the sister taxon to the rest of Artiopoda.

The early Cambrian (Series 2, Stage 3) Sirius Passet locality (North Greenland) is an important Burgess Shale-type Lagerstätte for understanding early animal life (Conway Morris *et al.* 1987; Harper *et al.* 2019). Fossils from this locality include new stem members of major phyla, importantly in this context, panarthropods (Budd 1993, 1998a, 1998b; Budd & Peel 1998; Vinther *et al.* 2016; Young & Vinther 2017; Park *et al.* 2018). Panarthropods are abundant and diverse in the Sirius Passet biota (Williams *et al.* 1996; Taylor 2002; Stein *et al.* 2010; Vinther *et al.* 2014; Nielsen *et al.* 2017; Harper *et al.* 2019). Artiopodans comprise most of the panarthropod diversity (Budd 1995, 1998a, 1998b, 1999, 2011; Babcock & Peel 2002, 2007; Lagebro *et al.* 2009; Peel & Stein 2009; Stein 2010; Stein *et al.* 2013; Peel 2017a), with several species still undescribed. The high artiopodan diversity is of interest because it may offer an opportunity to resolve their early evolution.

Here, we describe the novel artiopodan *Thulaspis tholops*, and recover it as the sister taxon to *Squamacula* in most analyses. This pair of genera is sometimes recovered as a sister group to the rest of Artiopoda and therefore presents a potential root to the group with a bearing on understanding the origins of Artiopoda.

MATERIAL AND METHOD

The current material was collected during the 2011, 2016 and 2017 field seasons and is accessioned to the Natural History Museum of Denmark, Copenhagen, Denmark (MGUH). Eight specimens of *Thulaspis* have been studied, of which three have part and counterpart available; these include various sizes and preservational states.

Exceptionally preserved fossils in the Sirius Passet Lagerstätte occur in a narrow unit of dark-grey mudstone and siltstones deposited in the distal part of the Buen Formation (Peel & Ineson 2011). Sirius Passet is unique for its high fossil density and frequent preservation of labile panarthropod soft tissues such as mineralized muscles and digestive structures, and organically preserved nervous tissues (Budd 2011; Peel 2017b; Young & Vinther 2017; Park *et al.* 2018; Nielsen *et al.* 2022). The rock unit is significantly altered by metamorphism (Topper *et al.* 2018; Nielsen *et al.* 2022). Non-mineralized arthropods are generally preserved as carbonaceous compressions with auxiliary three-dimensional phosphatization of features such as muscles and digestive systems, now partially replaced by metamorphic quartz and silicates (Nielsen *et al.* 2022). Relief offers the easiest way to identify most external morphological features given the significant alteration and loss of organic matter (Topper *et al.* 2018). Many arthropod taxa from Sirius Passet have ubiquitous wrinkles reflecting the rigidity of the cuticle during compactional stress. These compaction wrinkles and their orientation and density also offer insights into the relative depth of the skeleton (Budd 1999).

Observations and drawings

Photographs were taken with a Nikon D7100 digital camera with a Nikon AF-S VR 105 mm f/2.8G IF-ED micro-lens using low-angle lighting or polynomial texture mapping (PTM), also known as reflectance transformation imaging (RTI). Specular enhancement was used after PTM to digitally enhance the low relief of some specimens. Some specimens were coated in magnesium oxide prior to photography. Drawings were made with camera lucida, and digital illustrations were created using GIMP software before being vectorized in Inkscape.

Phylogenetic analyses

The character matrix from Zhang *et al.* (2022) was used in the phylogenetic analyses, with *Squamacula buckorum* Paterson *et al.*, 2012 and *Thulaspis tholops* added to form a matrix composed of 67 taxa and 93 characters (Table S1; Berks *et al.* 2023). Bayesian analysis was run in MrBayes version 3.2.7 for 10 million generations with four chains using the Monte Carlo Markov-chain discrete morphological character model, with sampling every 1000 generations and 25% burn-in resulting in 7500 retained samples. Parsimony analyses were run in TNT (Goloboff *et al.* 2008) with New Technology Search using the Sectorial Search, Ratchet, Drift and Tree-fusing algorithms with

default settings (Goloboff 1999; Nixon 1999). The search was set to collapse trees after every search and to find the minimum tree length 100 times. All of the characters were treated as unordered. Analyses were carried out with equal weights, as well as different implied weights ($k = 3$, $k = 5$ and $k = 10$), to enable assessment of homoplasy penalization on the topology. Symmetric resampling was carried out on more than 1000 replicates of a traditional search with a 33% change of probability; this provided nodal support values.

Institutional abbreviations. MGUH, Geological Museum, Natural History Museum of Denmark.

SYSTEMATIC PALAEOLOGY

EUARTHROPODA Lankester, 1904
ARTIOPODA Hou & Bergström, 1997
Genus THULASPIS nov.

LSID. <https://zoobank.org/NomenclaturalActs/B3E562E0-D025-4018-BF56-F573974B54C7>

Type species. *Thulaspis tholops* from the lower Cambrian (Series 2, Stage 3) Sirius Passet Lagerstätte, Buen Formation, Peary Land, North Greenland.

Derivation of name. Greek: *Thule*, the term given to the northernmost lands, and *aspis*, shield; with the intended meaning of 'shield of the northernmost lands'.

Diagnosis. As for type and only species.

Thulaspis tholops sp. nov.
Figures 1–9

LSID. <https://zoobank.org/NomenclaturalActs/639E124B-D37E-4510-9515-20ADDC5B21C6>

Derivation of name. Greek: *thólos*, dome, and *ops*, face; in reference to the reconstructed domed anterior of the head shield.

Diagnosis. Non-mineralized arthropod with ovate outline and 15 thoracic segments. Wide, semi-circular head shield about one-quarter the total length of the animal with small rounded genae. Anteriormost tergite bears slightly rounded spatulate pleural tips while posterior pleura increasingly curve backwards into short spines. Anteromedial expansions are present on the first five thoracic tergites and reduce in sagittal length distally. Tergites have substantial overlap axially and near the pleural tips. Pygidium is small and smooth, one-thirteenth of the total length and one-fifth of maximum width. Biramous limbs have broad, flap-like exopods with marginal setae.

Holotype. MGUH 34172a–b.

Paratypes. MGUH 34173a, 34174, 34175a, 34176–34179.

Other material. MGUH 34173b, 34175b.

Occurrence. Lower Cambrian (Series 2, Stage 3) Sirius Passet Lagerstätte, Buen Formation, Peary Land, North Greenland.

Description

General morphology. *Thulaspis tholops* is large with an ovate outline and a non-mineralized, yet evidently rigid exoskeleton (Figs 1, 2) in comparison with other artio podan taxa from the same locality. The largest specimen is the holotype (MGUH 34172), which has a maximum width of 87 mm at the third thoracic segment, and is at least 120 mm long despite missing the caudal region and last thoracic tergite. The smallest specimen (MGUH 34173a) is 68 mm long and 47 mm wide (Fig. 3). The exoskeleton is convex and has a somewhat raised axial region relative to the pleural regions.

Cephalon. Head shield has a broad semi-circular outline, almost as wide as the thorax and slightly more than one-fifth of the total length (Figs 1, 4). Densely packed ridges and furrows running parallel to the anterior border suggest that it was anteriorly domed in life and later compacted during diagenesis (Figs 1, 2, 4). Genae are small and rounded. Posterior margin of the head shield is convex and overlaps one-third of the first thoracic tergite's axis with very little overlap at the genae. Eyes have not been identified in any of the specimens, probably due to the lack of visible ventral morphology; however, a pair of bulbous mineralized structures present on both sides of the head shield in MGUH 34175a could speculatively represent mineralized internal moulds of eyes (Fig. 5), although their appearance is highly irregular.

Thorax. Thorax consists of 15 segments (Figs 1, 4). Anterior tergites curve slightly forwards but then curve increasingly backwards posteriorly, with the fourth and fifth tergites being roughly straight. Articulating half-ring-like structures, interpreted from anteromedial expansions separated from the main tergite by a faint furrow (Figs 2F, 3D), are present on the first five tergites, decreasing in sagittal length posteriorwards (Figs 1, 2F, 3D); they span slightly more than half the tergites' transverse width and may mark the lateral extent of the axis. The medial expansions mean that axial overlap between tergites decreases posteriorly from slightly more than one-quarter between the first two tergites to approximately one-sixth between the sixth and seventh tergites; an overlap that continues posteriorly to between the 10th and 11th tergites, after which the overlap increases to one-third between the 14th and 15th tergites. Pleural overlap is equal to the axial overlap between all except the first five thoracic tergites, where the overlap is less: approximately one-sixth their exsagittal length (Figs 1, 2). Anterolateral margins of the pleura gently curve into convex lateral margins in the first two tergites, then into a roughly straight margin on the third, followed by slightly concave lateral margins on the remaining

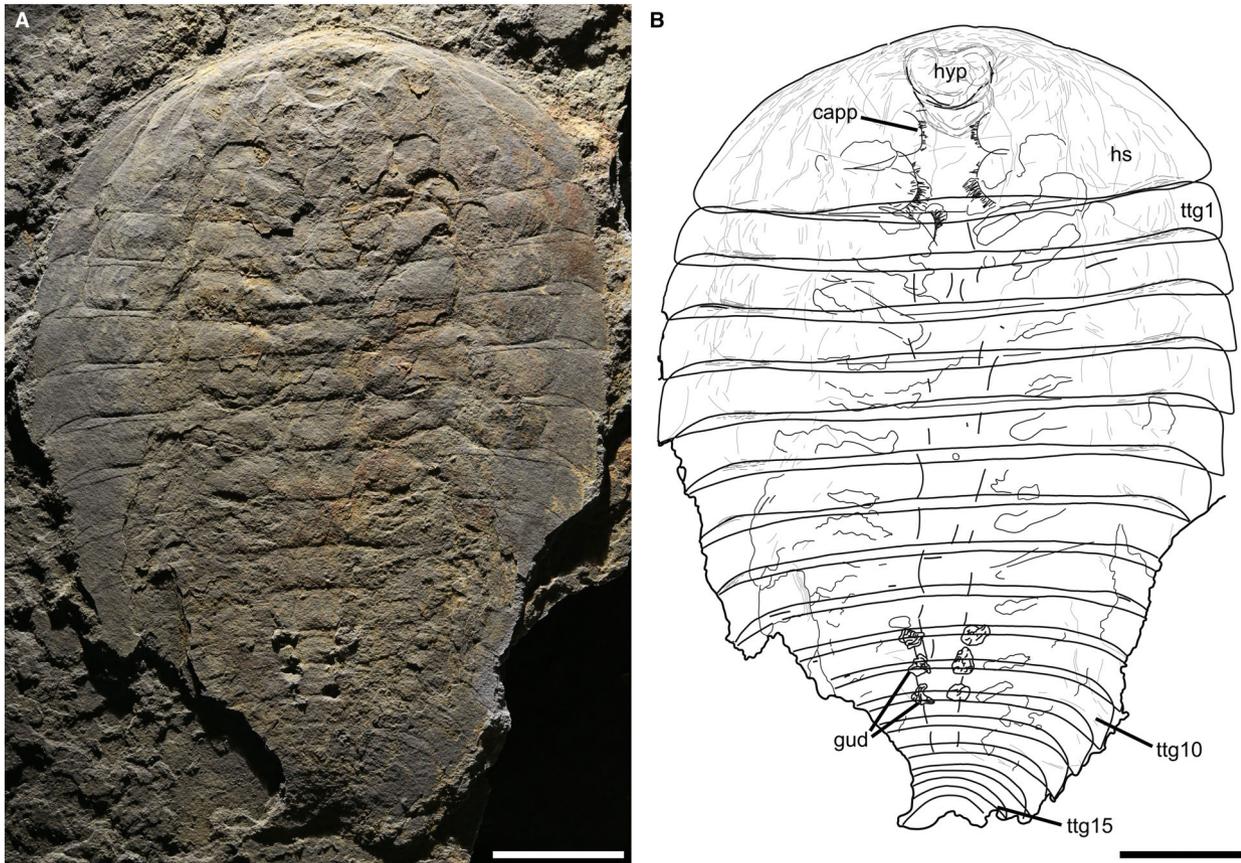


FIG. 1. *Thulaspis tholops* gen. et sp. nov. from the early Cambrian (Series 2, Stage 3) Sirius Passet Lagerstätte (North Greenland). MGUH 34172a, holotype. A, photograph. B, interpretive camera lucida drawing of A. *Abbreviations:* capp, cephalic appendage; gud, gut diverticulum; hs, head shield; hyp, hypostome; ttg, thoracic tergite. Scale bars represent 20 mm.

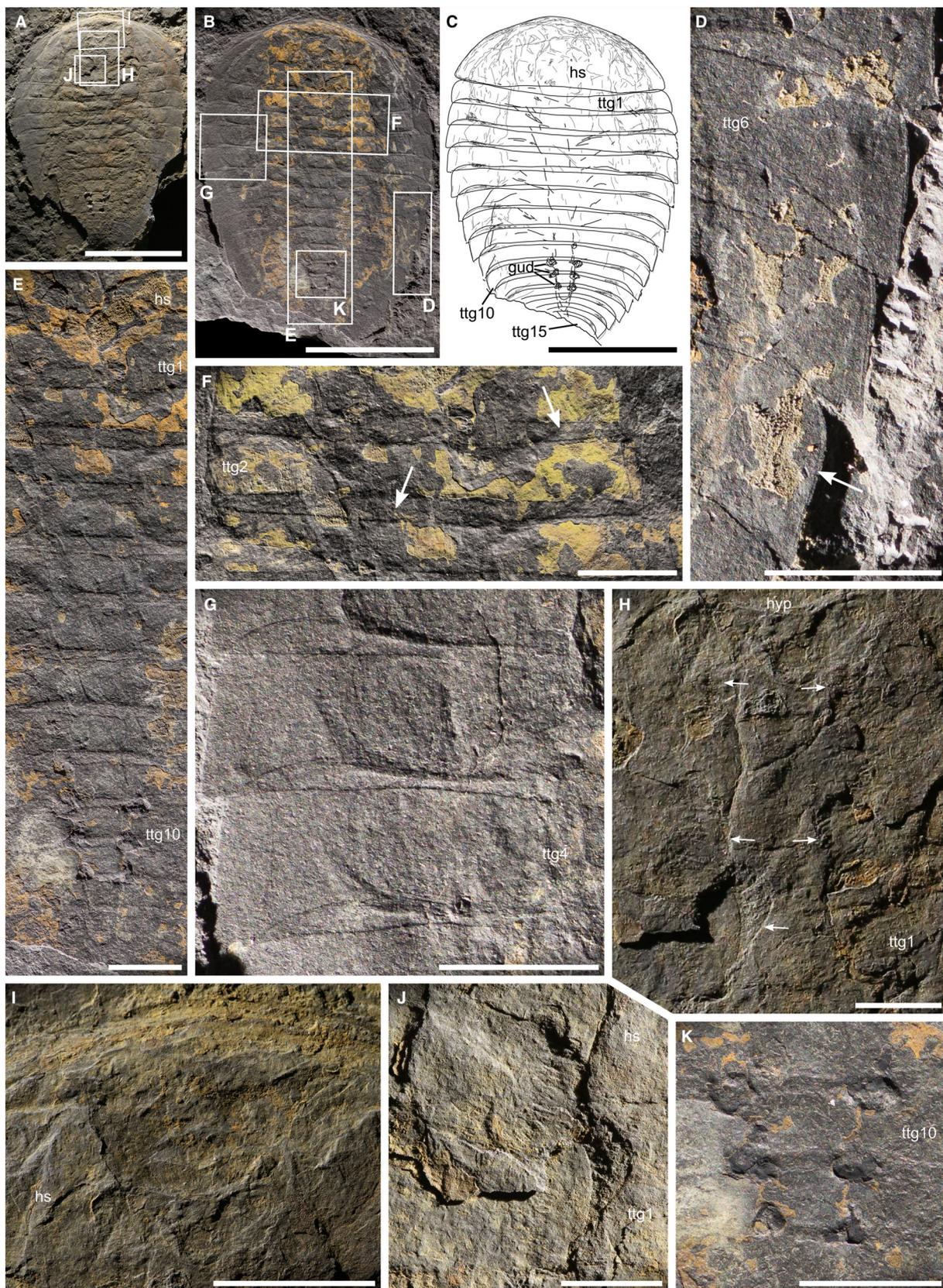
pleura (Figs 2D, G, 4C). The posterolateral corner of the tergites changes from rounded in the anteriormost tergites, producing a slight spatulate shape, to pointed at the third or fourth tergite and then increasingly spine-like posteriorwards. Pleural doublures are preserved to various degrees, running parallel close to the lateral margins of the pleura (Fig. 2D). Traces of the arthro-dial membranes between segments are present as thin, lined bands extending from the anterior margin of each post-cephalic tergite (Fig. 1). These membranes are usually visible as a striated region (Fig. 2G) or a single, thinner, high-relief band (Fig. 3A), probably representing different degrees of compression or extension prior to preservation.

Pygidium. Pygidium is micropygous, occupying just less than one-thirteenth of the total body length and roughly one-fifth of

the maximum body width (Fig. 4). It is roughly ovate, with a sagittal length about two-thirds of the transverse width, being widest at about one-third of the length. The anterior one-fifth of the pygidium overlaps the posterior one-third of the 15th thoracic tergite. A faint, anteriorly curved groove, most visible abaxially, runs roughly parallel to the margin of the last thoracic tergite (Fig. 4D); its distance to the anterior margin is slightly less than the width of the 15th thoracic tergite. It is interpreted to reflect the fused segmental boundaries between the terminal piece and the anterior segment of the pygidium.

Appendages. A partial antenna is seen in one specimen with the base and tip obscured (Fig. 6D); the visible section is equal in sagittal length to the head shield and consists of at least 20 simple rectangular podomeres. Biramous limbs are preserved in the post-

FIG. 2. Anatomical details of *Thulaspis tholops* gen. et sp. nov. holotype specimen (MGUH 34172). A, photograph of MGUH 34172a; outlined areas are magnified in H–J with a larger image available in Figure 1A. B, photograph of MGUH 34172b; outlined areas enlarged in D–G, K. C, interpretive camera lucida drawing of B. D, posterior pleural tips with arrow pointing to pleural ridge. E, axis, showing impaction of sternites. F, anteromedial tergal expansions, arrows point to furrows separating expansion from the main body of the tergite. G, arthro-dial membranes connecting adjacent pleura. H, gnathobasic structures in two pairs associated with the head shield and one of a pair associated with the first thoracic segment, arrows point to striations that represent spines extending adaxially from the protopodites. I, hypostome. J, gnathobasic protopodites. K, gut diverticula. *Abbreviations:* gud, gut diverticulum; hs, head shield; hyp, hypostome; ttg, thoracic tergite. Scale bars represent: 50 mm (A–C); 10 mm (D–G, K); 5 mm (H, J); 2 mm (I).



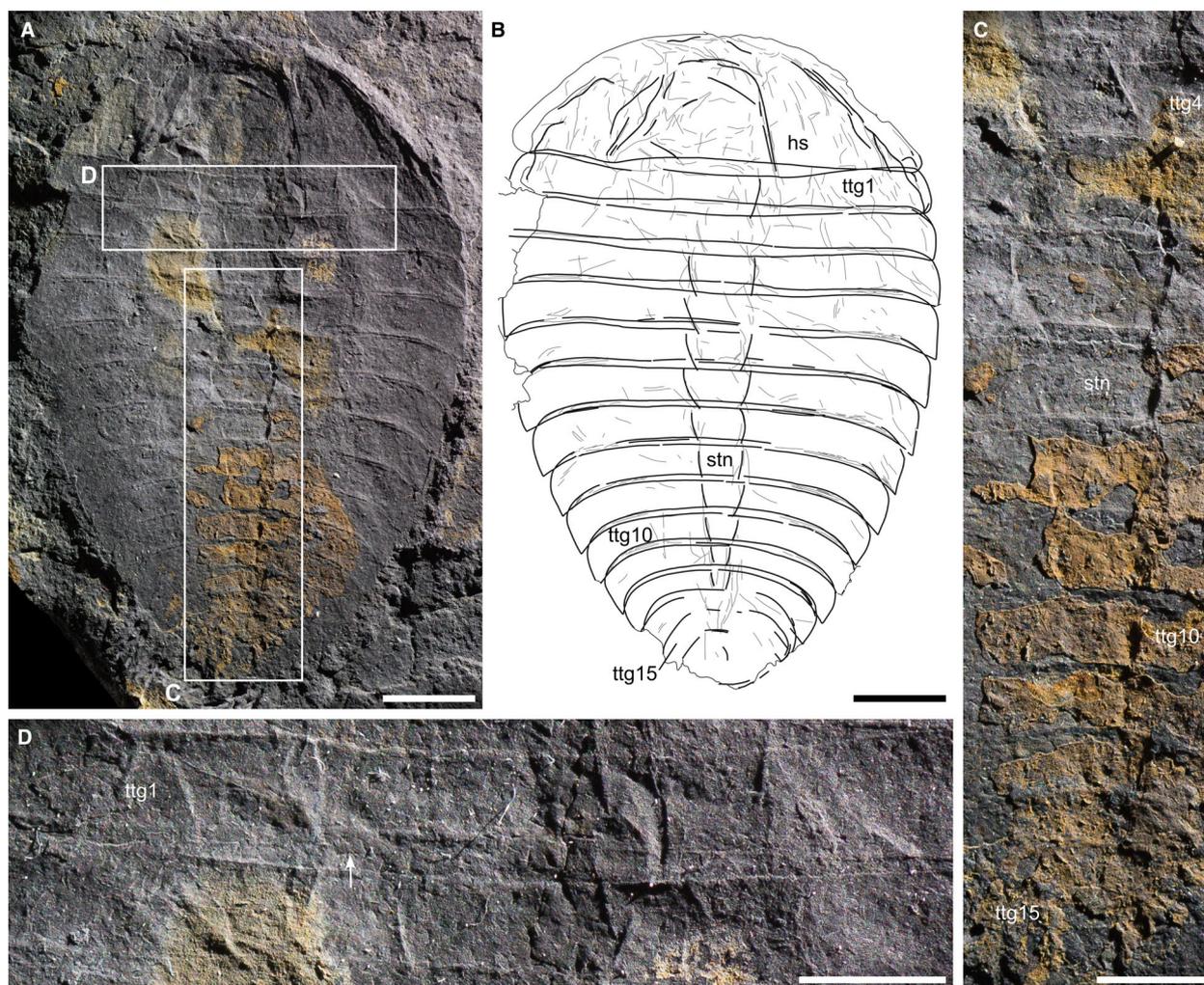


FIG. 3. The smallest specimen of *Thulaspis tholops* gen. et sp. nov. with sternite impressions (MGUH 34173a). A, photograph; out-lined areas enlarged in C–D. B, interpretive camera lucida drawing of A. C, axis showing clear impressions of sternites. D, anteromedial tergal expansion, arrow points to furrow separating expansion from main body of tergite. *Abbreviations:* hs, head shield; stn, sternite; ttg, thoracic tergite. Scale bars represent: 10 mm (A, B); 5 mm (C, D).

antennal cephalic segments and at least the first 11 thoracic segments (Fig. 6). Exopods are large round flaps with an exsagittal width about twice the exsagittal length of their associated tergite (Figs 7, 8D); they bear a fringe of short setae on the presumed dorsal edges, up to 1 mm in length (Figs 7D, E, 8E). Endopods extend slightly further from the body than the exopods (Fig. 6E), although detailed anatomy cannot be determined given that these structures are less frequently preserved and discerned. Gnathobasic spines up to 2 mm long are exposed on protopodites of the two post-antennal segments and the first thoracic segment (Fig. 2H, J). The presence of the two pairs of protopodites on the head shield of MGUH 34172a and two exopods extending from one side of MGUH 34178 (Fig. 8D) suggest that *Thulaspis* had two pairs of post-antennal cephalic appendages.

Internal anatomy. The gut tract begins in the middle of the cephalon and the presence of gut diverticula suggests that it continued to at least the 12th thoracic segment (Figs 2K, 5). The

cephalic portion appears to be widened (Fig. 5), possibly representing a crop. Carbonized subtriangular structures extending to the 10th thoracic segment in MGUH 34179 (Fig. 9) could be gut diverticula or, given their transverse width, triangular extensions surrounding the gut. Paired black axial nodules that line the articulations between tergites 10 and 12 in MGUH 34172 are interpreted here as phosphatized gut diverticula (Fig. 2K). Together these specimens suggest that the gut is likely to have possessed diverticula extending at least to the 12th thoracic segment.

Hypostome. A hypostome is visible with the most complete discernible outline in MGUH 34172a, where its margins are demarcated by compaction wrinkles against the head shield, with a particularly high relief and distinct set of wrinkles probably representing an anterior lobe (Fig. 2I). Anterior margin is less clear but appears to be slightly concave, resulting in an overall heart-shaped outline. The total sagittal length of the hypostome is only slightly larger than its transverse width, with the anterior

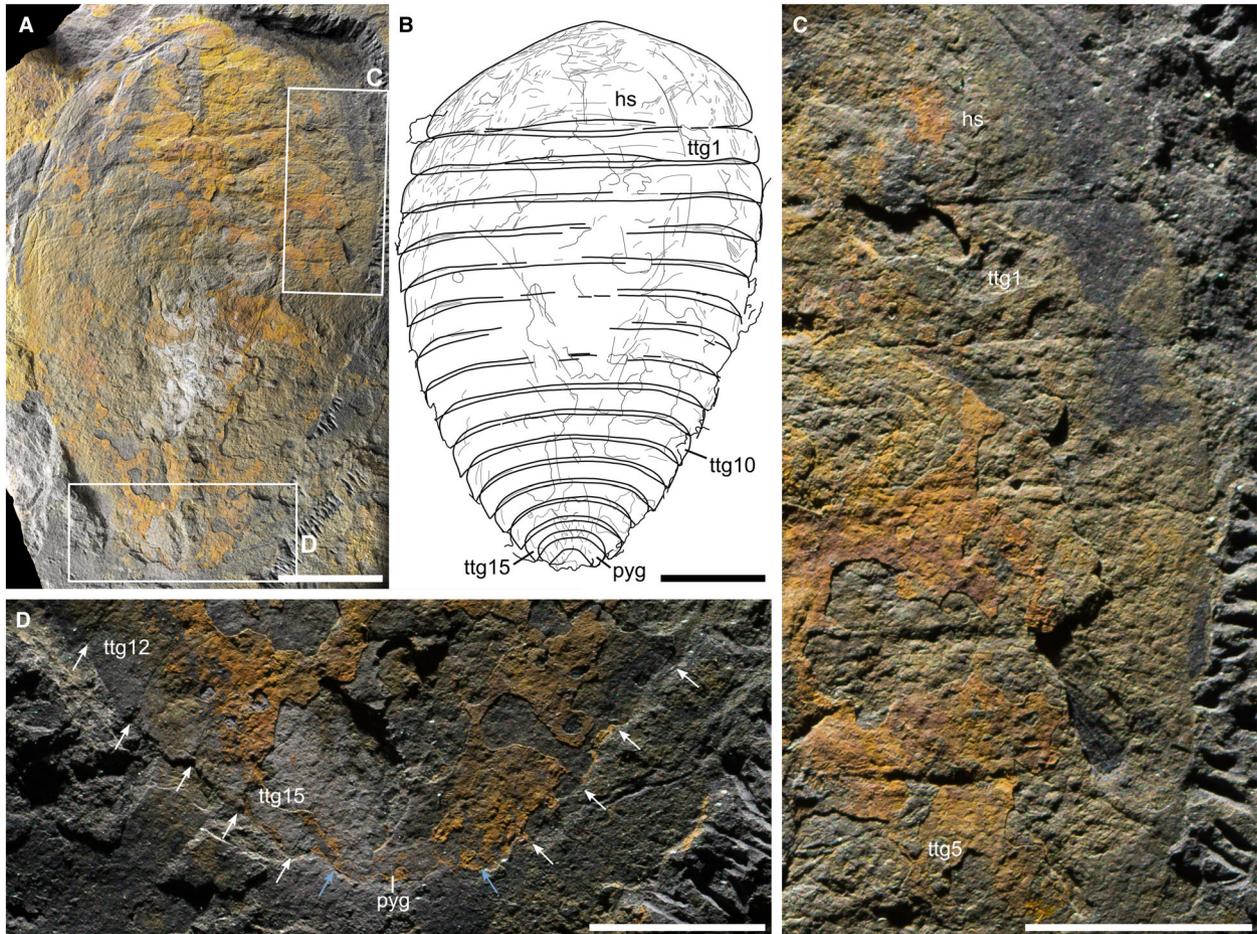


FIG. 4. Fully articulated dorsal aspect specimen of *Thulaspis tholops* gen. et sp. nov. showing caudal anatomy (MGUH 34174).

A, polynomial texture mapping (PTM) image using Static Multi Light rendering mode; outlined areas enlarged in C–D. B, interpretive camera lucida drawing of A. C, gena and anterior pleura, showing the transition from rounded to short spine. D, posterior thoracic tergites and pygidium, white arrows show boundaries between tergites and blue arrows point to the faint effaced pygidial joint. *Abbreviations:* hs, head shield; pyg, pygidium; ttg, thoracic tergite. Scale bars represent: 20 mm (A, B); 10 mm (C, D).

lobe's posterior margin forming a semi-circular curve, with a medial apex positioned at roughly seven-tenths of the total hypostome length from the anterior. Transverse width is about one-sixth of cephalic transverse width and sagittal length is about nine-twentieths of the cephalic sagittal length. It is uncertain whether the hypostome is directly attached to the cephalic margin or whether an anterior sclerite is present. The posterior part of the hypostome aligns with the gnathobases of the first post-antennal cephalic appendage pair.

Sternites. Axially positioned structures running throughout the thorax can be seen in several of the specimens (Figs 2E, 3C, 6C, 8C). They superimpose dorsal tergite articulation, suggesting that they are ventral, and are therefore interpreted as sternites. Their shape and overlap vary, ranging from subrectangular to trapezoid, probably due to taphonomy. None appears to have an hourglass shape.

Remarks. *Thulaspis* is morphologically broadly similar to *Squamacula* (Hou & Bergström 1997; Zhang *et al.* 2004; Paterson

et al. 2012), with a large, broad cephalon, 15 thoracic segments and a small pygidium. However, there are several key differences and a substantial size difference. *Squamacula* has a maximum length of only 32 mm, smaller than the smallest known specimen of *Thulaspis* and one-quarter the length of the largest. The large ventral structure, interpreted as a cephalic doublure, is a key feature of *Squamacula* that has not been identified in *Thulaspis*. Furthermore, the rounded genae and the pleural tip of the first thoracic tergite of *Thulaspis* differ from the acutely angled genae and pleural tips of either species of *Squamacula*. *Squamacula* also have not been found to have the anteromedial tergal expansions that are present in the first five thoracic tergites of *Thulaspis*. Another potential difference between the genera is in caudal morphology. The caudal region of *Squamacula* has been debated, with recent interpretations favouring a pygidium composed of a single segment and a terminal piece with two pairs of ventral appendages (Zhang *et al.* 2004; Paterson *et al.* 2012) over a single terminal tail shield (Hou & Bergström 1997). Despite some uncertainty in *Squamacula*, we find evidence that the caudal region of *Thulaspis* was also

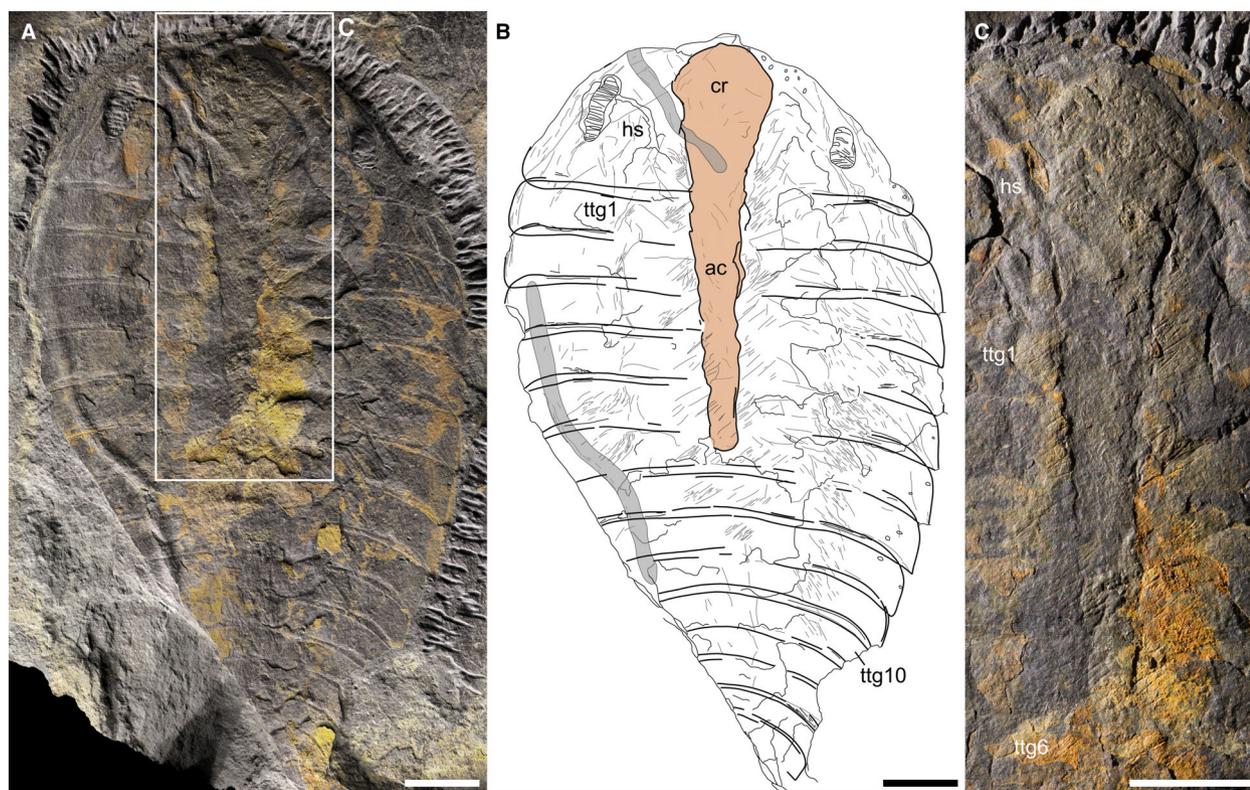


FIG. 5. *Thulaspis tholops* gen. et sp. nov. specimen showing phosphatized gut (MGUH 34175a). A, polynomial texture mapping (PTM) image using Static Multi Light rendering mode; outlined area enlarged in C. B, interpretive camera lucida drawing of A with orange colour representing the preserved gut and grey representing diagenetic trace fossils. C, alimentary canal with widened structure associated with head shield interpreted as a crop. *Abbreviations:* ac, alimentary canal; cr, crop; hs, head shield; ttg, thoracic tergite. Scale bars represent 10 mm.

composed of a single segment and a terminal piece, although the fused joint has not been completely effaced.

Phylogenetic analysis results

Thulaspis was consistently recovered as the sister taxon to *Squamacula* spp. in all phylogenetic analyses except the equal weights parsimony analysis (Figs 10, 11). All three implied weights analyses recover this pair of taxa as the sister taxon to the rest of Artiopoda. Bayesian analysis recovered this clade as part of a large clade at the base of Artiopoda with most major artiopodan clades also branching from this polytomy, although Protosutura was not recovered. Equal weights analysis failed to resolve *Thulaspis* and *Squamacula* as a clade, instead resulting in both genera being parts of another polytomy at the base of Artiopoda along with the genera of Protosutura and two clades: one formed by *Retifacies* (Hou *et al.* 1989) and *Pygmaclipeatus* (Zhang *et al.* 2000), and the other, the rest of Artiopoda. The newly added *Squamacula buckorum* was found as the sister taxon of *Squamacula clypeata* in all analyses.

DISCUSSION

The morphological interpretations of *Thulaspis tholops* from the specimens available are summarized in Figure 12

as reconstructions. At first glance the morphology of *Thulaspis* appears typical for Cambrian non-trilobite artiopodans, with many similarities to the genus *Squamacula* including a large, broad head, small pygidium and large, round exopods bearing fringes of short setae. With that being said, *Thulaspis* is unique among artiopodans with only two pairs of post-antennal cephalic appendage pairs. Furthermore, the anteromedial tergal expansions on the first five thoracic segments are an unusual feature and both the sternites and hypostome have novel morphologies for the group. Our detailed understanding of the morphology of *Thulaspis* should enable us to make inferences about its life ecology as well as to further clarify artiopodan relationships and evolution.

Palaeoecology

The seemingly quite robust endopods and wide body suggest that *Thulaspis* spent much of its life on the ocean floor. However, the very large, flap-like exopods are likely to have been capable of substantial propulsion, enabling *Thulaspis* to swim. These exopods will produce more drag during recovery strokes and are perhaps less efficient for

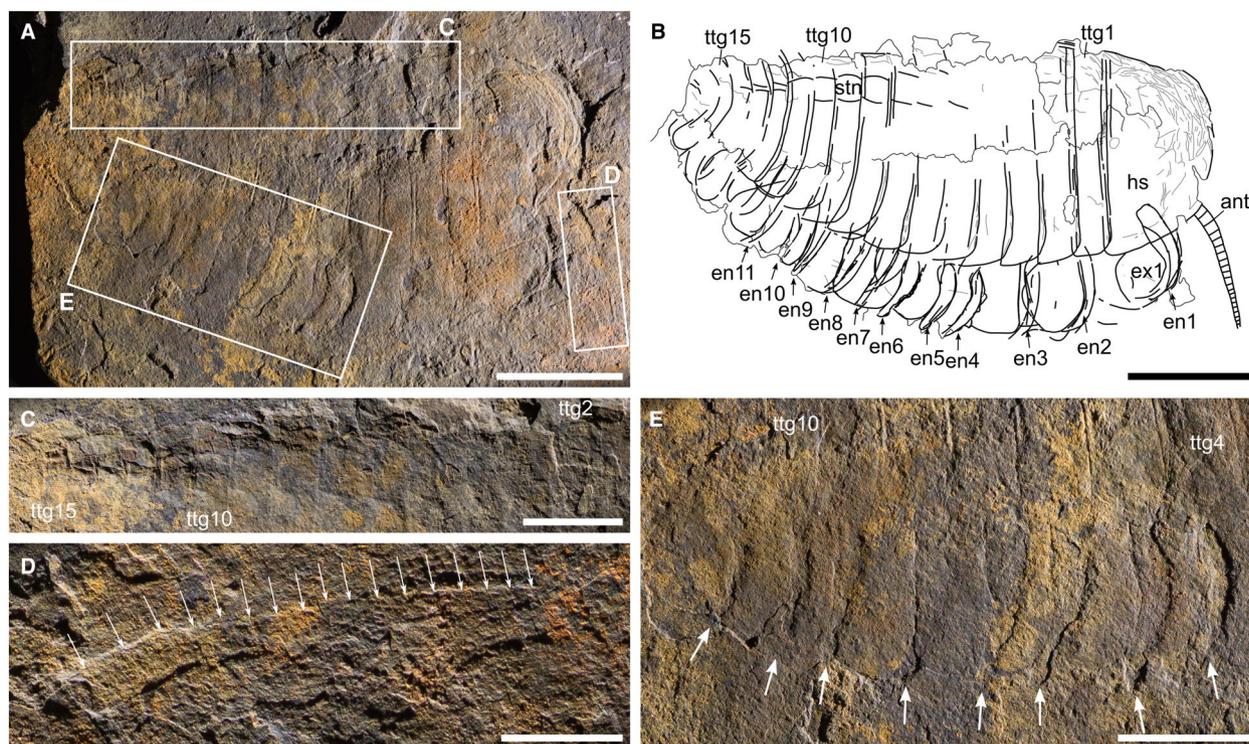


FIG. 6. Obliquely flattened specimen of *Thulaspis tholops* gen. et sp. nov. showing biramous appendages and antenna (MGUH 34176). A, photograph; outlined areas enlarged in C–E. B, interpretive camera lucida drawing of A. C, axis showing sternite impressions. D, antenna with arrows indicating joints between podomeres. E, thoracic appendages, arrows indicate endopods. *Abbreviations:* ant, antenna; en, endopods; ex, exopod; hs, head shield; str, sternite; ttg, thoracic tergite. Scale bars represent: 20 mm (A, B); 10 mm (C, E); 5 mm (D).

prolonged swimming than exopods with multiple paddle-shaped lamellae such as *Naraoia* Walcott, 1912 (Haug & Haug 2016) and *Pygmaclypeatus* (Schmidt *et al.* 2022). Together, we interpret *Thulaspis* as nektobenthic; perhaps mostly with a benthic lifestyle but capable of facultative swimming.

The rounded protopodites with elongate and thin gnathobasic spines are similar in morphology to those of the trilobite *Olenoides serratus* (Rominger, 1887), which has been shown to be adapted to process soft food sources (Bicknell *et al.* 2021). Both these taxa have gnathobases up to 2 mm long so it is possible that they used them to process very similar food items. The protopodites are relatively larger and more rounded than in most non-trilobite artio podans, many of which have quite slender or small protopodites (Chen *et al.* 2019; Lerosey-Aubril & Ortega-Hernández 2019; Schmidt *et al.* 2022); this is taken to the extreme in *Retifacies*, which bears smooth protopodites (Zhang *et al.* 2022). This might suggest that *Thulaspis* was undertaking more substantial food processing before ingestion than these taxa. The gnathobasic spines of *Squamacula clypeata* are much shorter, both in relative and absolute size, suggesting that they had different diets. The hypostome is relatively small

compared with the size of the head shield. Small, natant hypostomes are often found in supposed particle-feeding trilobites (Fortey & Owens 1999), although this is a functional conjecture of morphology. However, particle feeders are typically minute in size compared with *Thulaspis*. Although small relative to the head shield, the hypostome of MGUH 34172 is still *c.* 12 mm wide. This is easily big enough to accommodate a mouth that could ingest many soft-bodied organisms (e.g. ecdysozoan worms) found in the Cambrian, or even larger prey if processed by the gnathobases prior to ingestion.

Phylogenetic position and implications

Artiopoda are inherently difficult to root due to the lack of informative synapomorphic characters, leaving both internal relationships as well as external euarthropod phylogeny unresolved (Aria 2022). Some phylogenetic hypotheses have proposed *Squamacula clypeata* as a sister taxon to all other artio podans (Chen *et al.* 2019; Du *et al.* 2019; Schmidt *et al.* 2022; Zhang *et al.* 2022), while others have proposed *Retifacies* (Zeng *et al.* 2020; O'Flynn *et al.* 2022) or *Kiisortoqia* Stein, 2010 (Aria *et al.* 2020),

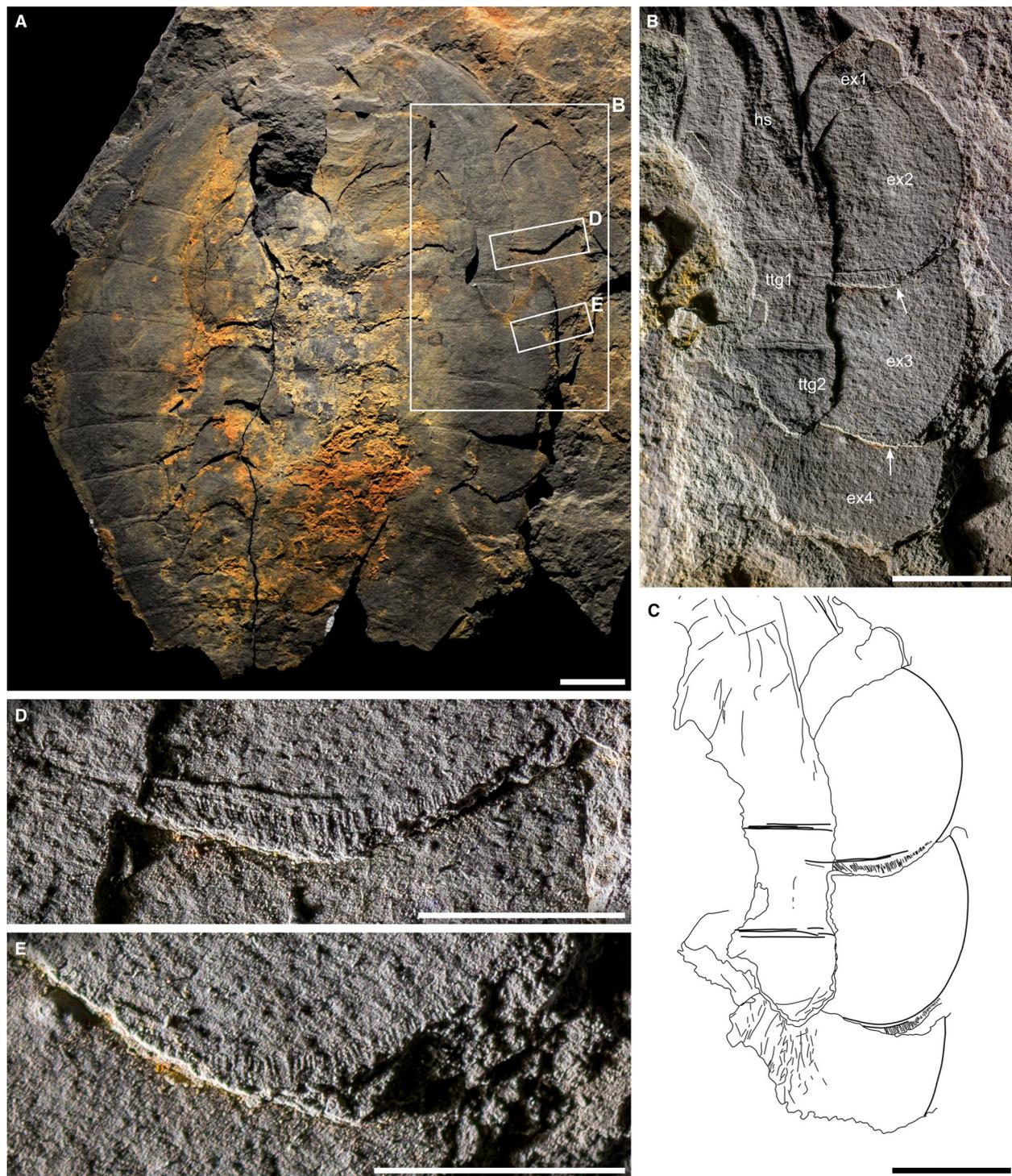


FIG. 7. Fragmentary specimen of *Thulaspis tholops* gen. et sp. nov. showing large exopods (MGUH 34177) A, photograph of specimen with fragmented parts placed together; outlined areas enlarged in B, D–E. B, fragment with exposed exopods bearing setae fringes (white arrows). C, interpretive camera lucida drawing of B. D–E, setae fringes on exopods. Abbreviations: en, endopods; ex, exopod; hs, head shield; ttg, thoracic tergite. Scale bars represent: 10 mm (A–C); 5 mm (D, E).

although the latter examples have limited arthropodan taxon sampling. Our analyses confirm the complexity of relationships between early arthropodans by resolving a

basal polytomy in the Bayesian and equal weights analyses in which *Thulaspis* and *Squamacula* feature. However, implied weight parsimony analyses consistently resolve

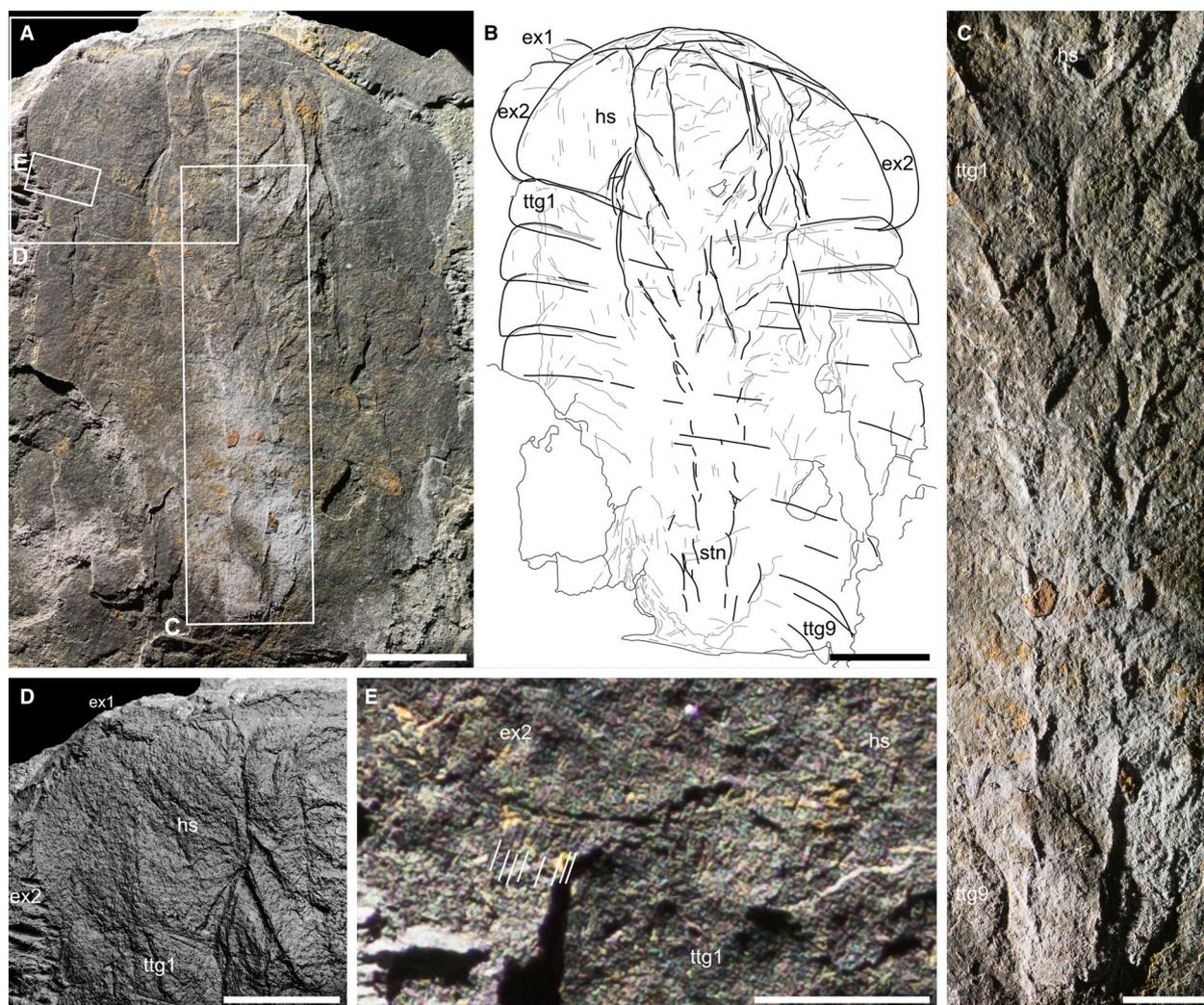


FIG. 8. Specimen of *Thulaspis tholops* gen. et sp. nov. showing cephalic exopods (MGUH 34178). A, photograph; outlined areas enlarged in C–E. B, interpretive camera lucida drawing of A. C, axis with impressions of sternites. D, polynomial texture mapping (PTM) image of cephalic exopods extending from underneath the cephalic shield in specular enhancement rendering mode. E, fringe of setae on cephalic exopod, white lines indicate the positions of individual setae. *Abbreviations:* ex, exopod; hs, head shield; stn, sternite; ttg, thoracic tergite. Scale bars represent: 10 mm (A, B, D); 5 mm (C); 2 mm (E).

Thulaspis and *Squamacula* as sister taxa to all other artiopodans. The consistent pairing of *Squamacula* and *Thulaspis* in our phylogenetic analyses suggests that the apparent similarities between them reflect a shared ancestry and therefore might inform on the ancestral body plan for Artiopoda despite not consistently resolving their exact position.

Squamacula has not always been recovered as the deepest branching artiopodan. With our results, and recent discoveries of other artiopodans, we can re-evaluate phylogenetic hypotheses for the root of Artiopoda and the positions of these enigmatic taxa. Stein *et al.* (2013) recovered *S. clypeata* in a clade with *Sidneyia* and Aglaspidida in their weighted analyses. Those findings may partly be an outcome of similar coding of the large ventral

cephalic structures in both *Squamacula* and *Sidneyia* interpreted as large doublures or hypostomes (Zhang *et al.* 2004; Stein 2013; Zacaï *et al.* 2016). We doubt that these structures are homologous and believe that further investigation and interpretation is warranted in the case of *Squamacula*. With that being said, the equal weights analysis from Stein *et al.* (2013) shows a rootward position for *Squamacula* in a large basal artiopodan polytomy, including several other taxa, such as *Retifacies*. Numerous recent studies looking at Cambrian arthropod phylogenetics have not included *Squamacula* and we believe that it, along with *Thulaspis*, *Retifacies* and *Pygmaclypeatus*, should be included in future analyses because they are likely to have deep branching positions that might help elucidate ancestral states of the clade.

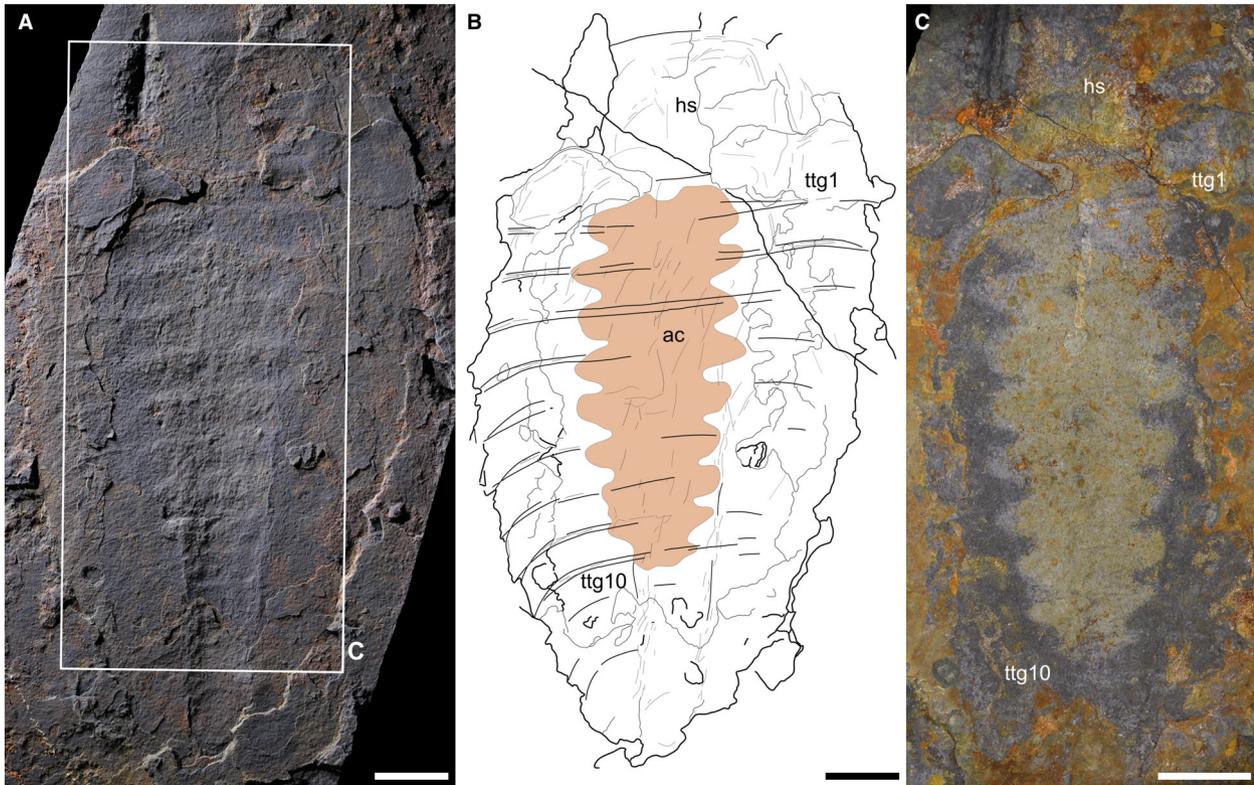


FIG. 9. *Thulaspis tholops* gen. et sp. nov. specimen showing gut trace with diverticula (MGUH 34179). A, photograph; outlined areas enlarged in C. B, interpretive camera lucida drawing of A with orange colour representing the preserved gut. C, axis with outline of carbonized gut including subtriangular structures. *Abbreviations:* ac, alimentary canal; hs, head shield; ttg, thoracic tergite. Scale bars represent 10 mm.

Retifacies has recently been resolved as a sister taxon to the rest of Artiopoda (Zeng *et al.* 2020; O'Flynn *et al.* 2022), although *Squamacula* was not included in these analyses. *Retifacies* is part of the clade Retifaciida Hou & Bergström, 1997, although the use of this name has recently been questioned (Zhang *et al.* 2022). We will use this name to refer to the clade composed of *Retifacies* as well as *Pygmaclypeatus*. These taxa share unusual multisegmented tailspines and similar thoracic exopod morphologies, with small exopodite lobes bearing a set of paddle-shaped lamellae (Hou & Bergström 1997; Liu *et al.* 2021; Schmidt *et al.* 2022). The original description of *S. clypeata* mentions that it may also belong to this clade (Hou & Bergström 1997), although this has recently been questioned due to lack of historic phylogenetic support (Zhang *et al.* 2022). Given our detailed morphological understanding of these taxa, it is clear that the retifaciid apomorphies are not seen in either *S. clypeata* or *Thulaspis*, therefore inclusion in Retifaciida seems unjustified. Without more detailed data for *S. buckorum* we cannot rule out an affiliation with Retifaciida, although its very similar tergal and doublure morphology to *S. clypeata* provides no reason to assume that their morphologies would vary substantially. Recent studies of

Chengjiang artiopodans have used micro-computed tomography (micro-CT) to reveal heteronomous appendicular morphology in taxa that were previously thought to exhibit limb homonomy based on traditional observation (Chen *et al.* 2019; Schmidt *et al.* 2022; Zhang *et al.* 2022). These studies subsequently suggested that limb heteronomy may be more widespread in Artiopoda than previously thought, and possibly an ancestral trait. The data available for *S. clypeata* (Zhang *et al.* 2004) and *Thulaspis* (Fig. 6) suggest that they show little variation in appendicular morphology, supporting the traditional view of Artiopoda; however, because micro-CT data are not available for *Squamacula* and given that Sirius Passet fossils are incompatible with micro-CT, we cannot confidently rule out the possibility of limb heteronomy. A couple of analyses have corroborated a close relationship of *Squamacula* with the retifaciids (Legg *et al.* 2013; Zhang *et al.* 2022), although most phylogenetic analyses have not (Paterson *et al.* 2010; Edgecombe *et al.* 2011; Chen *et al.* 2019; Du *et al.* 2019; Schmidt *et al.* 2022). Zhang *et al.* (2022) recovered *S. clypeata* with *Retifacies* and *Pygmaclypeatus* in their Bayesian analysis only, whereas past versions of this matrix and our updated version with *Thulaspis* and *S. buckorum* included have not

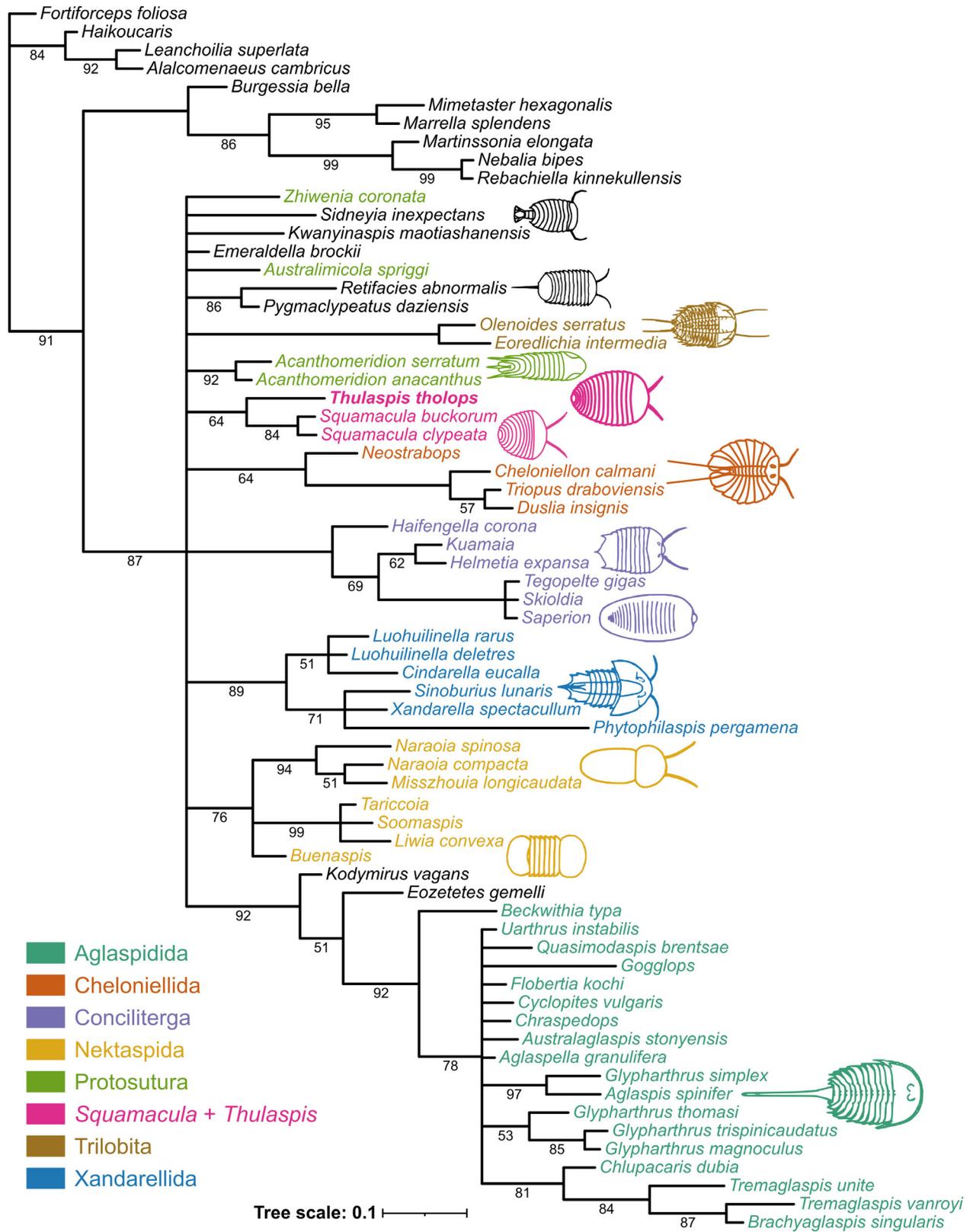


FIG. 10. Consensus tree result of Bayesian phylogenetic analysis with key clades and groups coloured according to legend and basic reconstructions of key taxa. Carried out in MrBayes using the Mk model, 10 000 000 generations, 4 chains, sampling 1 in 1000 generations with 25% burn-in (7500 samples retained). Posterior probability values are represented along branches.

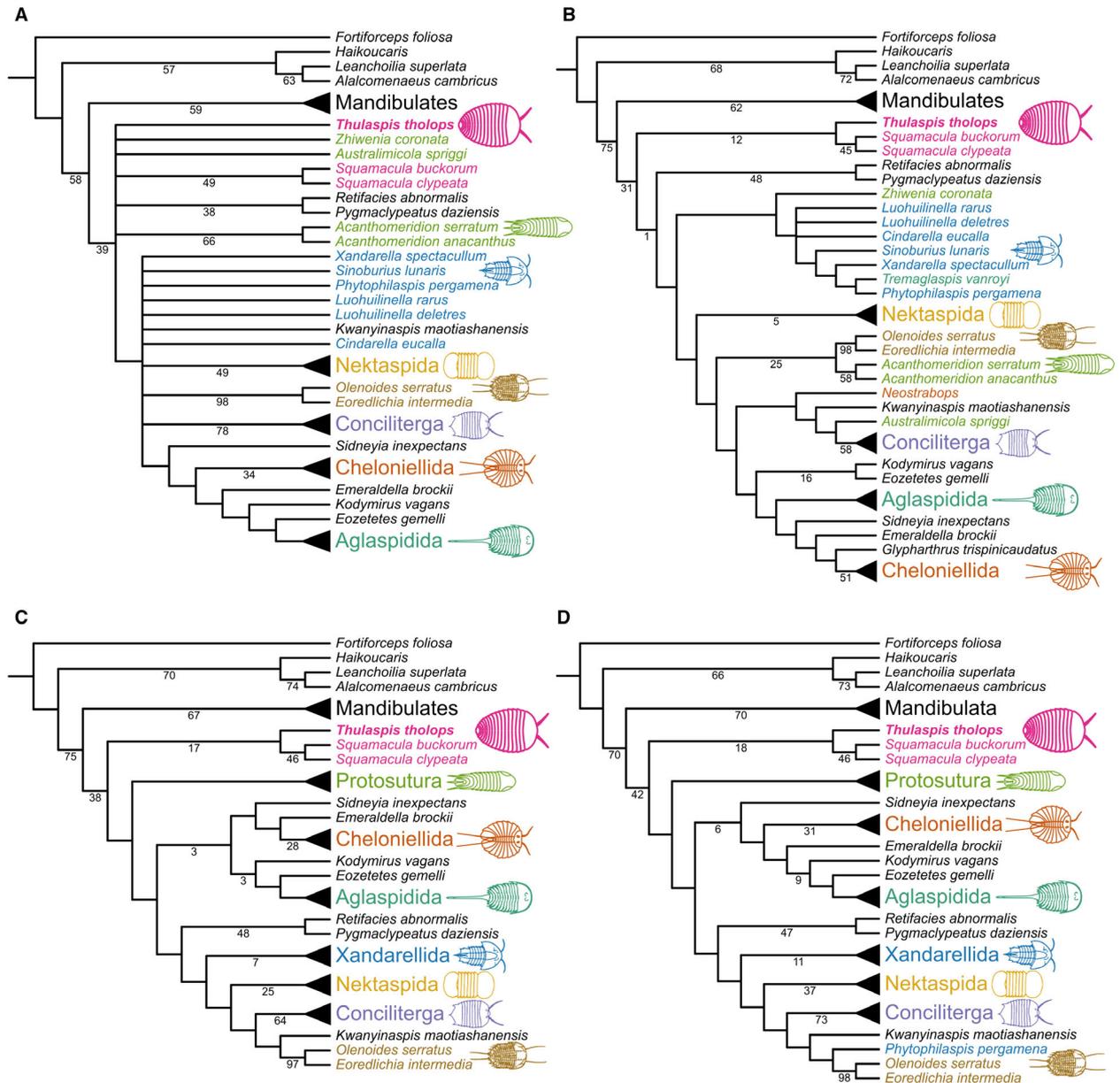


FIG. 11. Phylogenetic analysis results from TNT. A, equal weights analysis consensus tree from 27 most parsimonious trees (MPTs) (consistency index (CI) = 0.35, retention index (RI) = 0.66). B–D, implied weights trees: B, $k = 3$ consensus tree from 14 MPTs (CI = 0.38, RI = 0.70); C, $k = 5$ tree (CI = 0.40, RI = 0.72); D, $k = 10$ tree (CI = 0.41, RI = 0.73). Node support values calculated using symmetrical resampling represented along branches. Taxa are coloured based on the groupings in Figure 10.

produced this result. Legg *et al.* (2013) produced a large-scale early arthropod phylogeny with extensive artiopodan sampling; they found ‘Retificiida’ as sister to the rest of Artiopoda, although this included both species of *Squamacula* as well as *Kiisortoqia* and *Siriocaris* (Legg *et al.*, 2009). However, this analysis was done before the redescription of *Retifacies* (Liu *et al.* 2021; Zhang *et al.* 2022) and, more importantly *Pygmaclipeatus* (Schmidt *et al.* 2022), in which its appendicular morphology and multisegmented tailspine were described.

Kiisortoqia and *Siriocaris* are often omitted from analyses, hence their relationships are poorly understood. *Kiisortoqia* has also been recovered as the deepest branching artiopodan (Aria 2020; Aria *et al.* 2020), and also as even outside of Artiopoda (Stein *et al.* 2013; O’Flynn *et al.* 2022); however, the latter analyses used the interpretation of the first appendage pair as raptorial limbs rather than as sensory antennae, a hypothesis that has not been quantitatively tested. With that being said, neither has any distinct, identifiable apomorphies and therefore

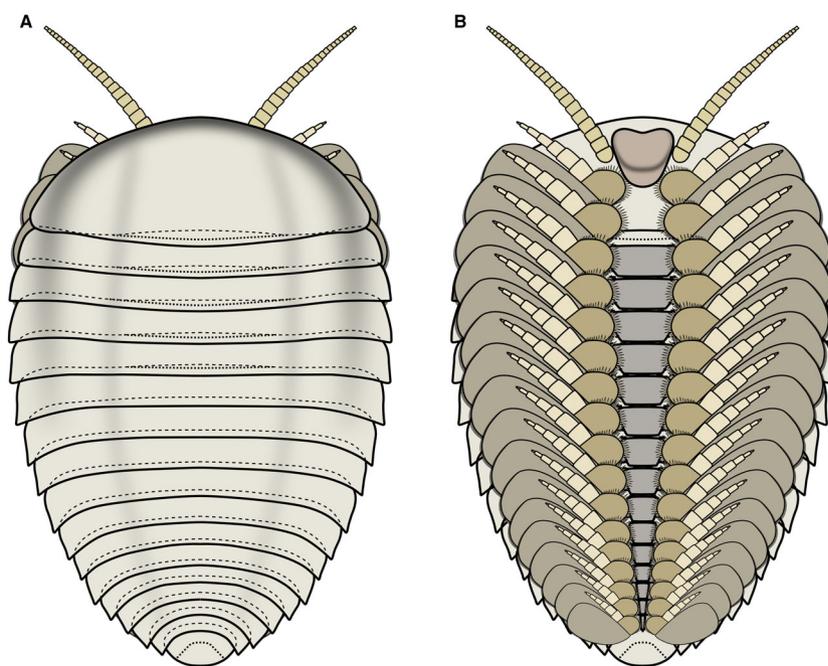


FIG. 12. Reconstruction of *Thulaspis tholops* gen. et sp. nov., showing post-antennal appendages using the appendages of *Squamacula clypeata* to help infer attachment of endopods and exopods to basipods (Zhang *et al.* 2004; Ortega-Hernández *et al.* 2013): A, dorsal view; B, ventral view.

deep branching positions are unsurprising. Both taxa also share similar large, flap-like exopod morphologies with *Thulaspis* and *S. clypeata*, which might suggest a close relationship of these taxa; however, convergent evolution is not unlikely, given the locomotive function. Further investigation into the phylogenetic relationships of these two taxa is likely to be important in understanding the root of Artiopoda.

Currently, several morphological matrices coding fossil arthropods exist. Their composition of taxa, characters and interpretations result in alternative hypotheses regarding which fossils occupy the euarthropod stem (Aria & Caron 2017) as well as the mandibulate (Scholtz & Edgecombe 2005; Ortega-Hernández *et al.* 2013; Stein *et al.* 2013; Zeng *et al.* 2017, 2020; Aria *et al.* 2020) and chelicerate (Legg *et al.* 2013; Vannier *et al.* 2018; Aria 2020) total groups. Artiopodans are similarly involved in this lack of consensus and ultimately may be affected by these alternative views. Fossils help break long morphological branches and hence deeper studies of early artiopodans may help resolve some of these debates. The matrix we have used does not include chelicerates given that they were removed from the outgroup in previously published iterations after Artiopoda was recovered in total-group Mandibulata (Ortega-Hernández *et al.* 2013; Lerosey-Aubril *et al.* 2017). In Legg *et al.* (2013) the ‘Retificiida’ clade, including *Squamacula*, was positioned at the root of Artiopoda in total-group Chelicerata. If the recovered position at the base of Artiopoda is accurate, then *Thulaspis*, in

combination with *Squamacula*, could be helpful for estimating the ancestral condition of the clade.

Thulaspis’ flap-like exopod with marginal setae is in line with what we would expect from ancestral exopod morphology because it is present in many outgroup taxa, including those regularly recovered or debated as stem Euarthropods such as megacheirans (Briggs & Collins 1999; Chen *et al.* 2004; Liu *et al.* 2021), fuxianhuides (Hou & Bergström 1997; Yang *et al.* 2013, 2018; Ortega-Hernández *et al.* 2018) and *Kylinxia* Zeng *et al.*, 2020. Assuming this morphology is ancestral to Euarthropoda, it is therefore not very helpful in resolving the position of Artiopoda because it is likely to be present in most deep branching taxa, including stem mandibulates and stem chelicerates. With that being said, most artiopodans have three or four post-antennal cephalic appendage pairs, making *Thulaspis* unusual, along with *Squamacula* and *Sidneyia*, which both have highly derived ventral cephalic morphologies. It is not clear what number of cephalic appendages would be ancestral to the group.

Typical artiopodan sternites were traditionally thought to be hourglass shaped (Ortega-Hernández *et al.* 2017). However, they are often poorly preserved or obscured by dorsal morphology (Stein 2010; Chen *et al.* 2019; Schmidt *et al.* 2022; Zhang *et al.* 2022). The sternites we have described for *Thulaspis* are distinctly not hourglass shaped. It is not clear which of these states is more likely to be plesiomorphic. Regardless, *Thulaspis*

expands the known morphologies of artiopodan sternites and shows that greater morphological variety might still be found.

The conjoined pygidium of *Thulaspis* is consistent with many of the other proposed early branching taxa. The joint of the two conjoined segments is not fully effaced, unlike the state proposed in *S. clypeata*. However, both of these taxa are micropygous, suggesting that this might be the ancestral state of artiopodans. This is contrary to the morphologies of *Retifacies* and *Pygmaclypeatus*, which are macropygous and subisopygous, respectively.

Although we do not know the exact attachment of the hypostome in *Thulaspis*, we can rule out an extension of the doublure given that there is a substantial gap between the hypostome and the anterior margin of the cephalon and no evidence of a wide doublure. This is contrary to the state currently described in *Squamacula* and in the retifaciids and several genera from across the tree, in which the hypostome is simply a medial expansion of the cephalic doublure (Hesselbo 1992; Cotton & Braddy 2003; Schmidt *et al.* 2022; Zhang *et al.* 2022). Given that this is currently expected to be the ancestral form of the hypostome, based on the taxa typically recovered as deep branching, *Thulaspis* presents a possible alternative origin for this key morphological feature. Alternatively, this may simply be an apomorphy of *Thulaspis*; this is corroborated by the unusual hypostome morphology with its concave anterior margin and anterior lobe. Whether the separate sections are simply morphological features of the hypostome or whether they represent separate elements that have fully or partially fused is unclear from the specimens so far found.

Thulaspis expands the known diversity of arthropods from the Sirius Passet Lagerstätte. As a close relative of the genus *Squamacula*, it is also likely to be one of the deepest branching artiopodans and its anatomy can therefore help us infer the ancestral morphology of this prolific clade. With future studies, *Thulaspis* and other possible deep branching artiopodans may be instructive in resolving their phylogeny and polarizing their morphological evolution.

CONCLUSIONS

1. We describe *Thulaspis tholops*, a new genus and species of Cambrian arthropod from the Cambrian Sirius Passet Lagerstätte in North Greenland, thereby expanding the known diversity of this fauna.
2. *Thulaspis* has a broad head, 15 thoracic segments and a small tail shield with biramous appendages bearing gnathobasic protopodites and large flap-like exopods with a margin of small setae.

3. We uncover a close relationship between *Thulaspis* and the enigmatic artiopodan *Squamacula* and find that these taxa are likely to branch deeply within Artiopoda.

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Author contributions. HOB and JV designed the research; HOB, MLN, T-YSP, JF-S and JV interpreted the fossil material. HOB, MLN and JF-S photographed the fossil material. HOB and JF-S drew the fossil specimens. HB constructed polynomial texture mapping images and carried out phylogenetic analyses. Transportation and accessioning of specimens was organised by MLN, ATN and JV. HB wrote the paper with input from the other authors.

DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains have been registered in ZooBank (<http://zoobank.org/references/8D6D232A-B5DD-40A3-9436-2E61A059F17F>). A phylogenetic character matrix for this study is available in Morphobank: <http://morphobank.org/permalink/?P4422>

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SUPPORTING INFORMATION

Additional Supporting Information can be found online (<https://doi.org/10.1002/spp2.1495>):

Table S1. Phylogenetic character matrix.

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