A problematic soft-bodied fossil from the Cambrian (Miaolingian, Wuliuan) of Utah

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Abstract

The Spence Shale of Utah and Idaho preserves a diverse soft-bodied biota from the Cambrian. While the fauna is dominated by arthropods and echinoderms, soft-bodied animals belonging to other groups are known. Here we document *Tentalus spencensis* gen. et sp. nov. from the High Creek locality of the Spence Shale. The fossil has a crown of short stubby tentacles and appears to have been attached to the sediment through a stalk. The morphology of *Tentalus* suggests that it is a dinomischiid or deuterostome, however it cannot be attributed to any of the known species, based on the short and conical tentacles surrounding an oral region, and polyp-like oblong columnar trunk terminating in a stalk, that do not resemble any described species

Keywords:
Great Basin; Lagerstätte; Laurentia; Spence Shale; filter feeding; Deuterostomia; *Dinomischus*

1. Introduction

The Cambrian exposures of the Great Basin yield several Fossil-Lagerstätten (*sensu* Kimmig & Schiffbauer, 2024) that have provided important information into the understanding of the early evolution of life. Among them the Spence Shale Lagerstätte (Spence Shale hereafter) of northeastern Utah and southeastern Idaho preserves one of the most diverse biotas of Laurentia (Briggs & Robison, 1984; Briggs *et al.* 2008; Kimmig *et al.* 2019a, 2023, 2024; Whitaker & Kimmig, 2020). Its fauna comprises over 100 species, of which about one-third are soft-bodied (Robison *et al.* 2015; Kimmig *et al.* 2019a, 2023, 2024; Whitaker & Kimmig, 2020; Whitaker *et al.* 2020, 2022). While the fauna is dominated by panarthropods and echinoderms, soft-bodied animals belonging to other groups are diverse, but rarely abundant (Robison et al. 2015; Kimmig *et al.* 2019a, 2023, 2024; Whitaker & Kimmig, 2020; Foster *et al.* 2022; Yang *et al.* 2025). Most of the soft-bodied taxa are limited to the Lagerstätten intervals in the Wellsville Mountains (Kimmig *et al*. 2019a; Whitaker & Kimmig, 2020), but other outcrops of the Spence Shale have yielded some soft-bodied taxa, with the High Creek locality north of Logan, Utah preserving the most abundant outside of the Wellsville Mountains (Kimmig *et al*. 2019a, 2023; Whitaker *et al.* 2022).

Here, we document and describe *Tentalus spencensis* gen. et sp. nov., a new putative dinomischiid or deuterostome known from a single specimen from the High Creek location of the Spence Shale (Cambrian, Miaolingian, Wuliuan) of Utah, USA. As this fossil is unlike any known Cambrian tentacle-bearing fossil (e.g., Caron *et al.* 2010; Conway Morris, 1977; Jin *et al.* 2006; Nanglu *et al.* 2023) or fossil from the Spence Shale we discuss its potential affinities.

2. Geological setting

The Spence Shale Member of the Langston Formation is regionally extensive with outcrops in southeastern Idaho and northeastern Utah (Fig. 1). The Spence Shale Member ranges in age from *Mexicella mexicana* to *Glossopleura walcotti* biozones (Cambrian, Miaolingian, Wuliuan, 507.5–506 Myr) (Liddell *et al.* 1997; Kimmig *et al.* 2019a), with all soft-bodied fossils to date coming from the *Glossopleura walcotti* Biozone. It was deposited on a slope on the passive western margin of Laurentia, as suggested by the wackestones, marls and siliciclastic mud-rich carbonate mudstones and contain some laminae of intercalated packstones (Kimmig *et al.* 2024) and outcrops record an overall increase in depth from Utah to Idaho. The Spence Shale Member ranges from ~9 m at Blacksmith Fork to ~120 m at Oneida Narrows (Walcott 1908; Deiss 1938; Liddell *et al.* 1997), and conformably overlies the Naomi Peak Limestone Member of the Langston Formation. The High Creek Limestone member of the Langston Formation in turn conformably overlies the Spence Shale Member.

The specimen was found in the middle of the Spence Shale Member at the High Creek locality in the Bear River Range, north of Logan Utah. Due to local faulting in the area, part of a larger fault system in northeastern Utah (Williams 1948; Valenti 1982; McCalpin 1994; Evans &

Oaks Jr. 1996; Black *et al.* 2000; Whitaker *et al.* 2022), it is unclear exactly at what height compared to the reference section (Fig. 1C). In the High Creek area, the Spence Shale exposes carbonate facies belts as well as transitional siliciclastic-carbonate facies (siliciclastic mud-rich, carbonate mudstones) of a Cambrian carbonate ramp system (Kimmig *et al.* 2024). The facies change up-section. The succession is interpreted as having been deposited in a ramp-like setting with minor relief, based on the absence of synsedimentary deformation features such as slumps. The succession, as a whole, reflects a decrease in water depth, as the progressive decrease in carbonate mud throughout the succession reflects an increase in depositional energy up-section. Based on the preserved fossil remains, there seems to be an increase in fossil abundance up-section, too, indicating an increase in biodiversity towards shallower water environments (Kimmig *et al.* 2024). SMNK-PAL 73174 was recovered from an interval of siliciclastic mud-rich carbonate mudstones.

3. Material and methods

The specimen was collected by Paul Jamison and is reposited at the Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany with a permit from the U.S. Department of Agriculture Forest Service to JK. The specimen was collected with hand tools.

The specimen was photographed with a Canon EOS R5 camera mounted with an EF 100 f/2.8 Macro IS USM lens. The specimen was photographed under white light and cross polarized light in two mediums—air and immersed in ethanol. Close-ups were captured using a Keyence VHX 7000 digital microscope under white light.

The color, contrast, and brightness of the images were adjusted using Adobe Photoshop. Line drawings were made with Adobe Illustrator. Specimen measurements were made from photographs in ImageJ (Schneider *et al.* 2012).

Institutional Abbreviations: KUMIP, Division of Invertebrate Paleontology, Biodiversity Institute, University of Kansas, Lawrence, USA; ROM and ROMIP, Royal Ontario Museum, Toronto, Ontario, Canada; SMNK, Staatliches Museum für Naturkunde Karlsruhe, Karlsruhe, Germany; USNM, National Museum of Natural History [United States National Museum], Washington, DC, USA.

4. Systematic paleontology

Phylum Uncertain

Tentalus gen. nov.

LSID. urn:lsid:zoobank.org:

Etymology. Tentalus after the fictional boss in the game The Legend of Zelda: Skyward Sword, in reference to its crown of tentacles.

Type species. Tentalus spencensis sp. nov.

Localities and horizon. As for the type species, by monotypy.

Diagnosis. As for the type species, by monotypy.

Tentalus spencensis sp. nov.

Figure 2

LSID. urn:lsid:zoobank.org:

Etymology. spencensis after the type deposit.

Holotype. SMNK-PAL 73174, part of laterally preserved specimen.

Locality and horizon. SMNK-PAL 73174 originates from the middle of the Wuliuan Spence Shale Member (*Glossopleura walcotti* Biozone) of the Langston Formation, High Creek locality, ~25 km north of Logan, Wasatch Range, Cache County, Utah, USA, Sec. 3 T13N, R02E (GPS: 41.896, -111.711).

Diagnosis. Solitary, with a whorl of at least 14 tentacles surrounding an oral region, polyp-like oblong columnar trunk terminating in a stalk. Tentacles are short and conical.

Description. The body of the holotype and only known specimen is 10.4 mm long and 7.2 mm wide. The body is oblong, preserves tentacles at the anterior end and tapers slightly at the posterior end.

The anterior end preserves at least 14 tentacles. The tentacles are conical in shape, and on average 2.7 mm long and about 0.9 mm at the base. Some tentacles preserve striations (Fig. 2D), which might represent pinnules. As the tentacles are all straight and elongated it is possible that they were relatively stiff, as has been suggested for *Dinomischus* (Zhao *et al.* 2019).

The posterior end of the calyx tapers and extends into a stalk that is about 2.4 mm wide. The stalk is poorly preserved and it is unclear how long it is, or if a terminal disc or holdfast were present.

Remarks. In over 60 years of fossil collecting at the High Creek locality this is the only specimen of *Tentalus spencensis* that has been found. It is unclear whether or not *Tentalus spencensis* had a long stalk and holdfast, as the lowermost part of the specimen is not preserved. It differs from *Siphusauctum lloydguntheri* Kimmig *et al.* 2017 by preserving a crown of short tentacles, a less tapering calyx, and the stalk of *T. spencensis* does not appear to have a division into an inner and outer layer. *T. spencensis* differs from *Dinomischus isolatus* Conway Morris 1977 from the Burgess Shale and Kaili biota, by preserving shorter tentacles and having less of a tapering calyx. *T. spencensis* differs from *Dinomischus venustus* Chen, Hou & Lu 1989 from the Chengjiang biota, by preserving shorter tentacles, the lack of a long central tubular structure, and less of a tapering calyx.

5. Discussion

5.a. Affinities of Tentalus spencensis

The appearance, but partial preservation of *Tentalus spencensis* gen et sp. nov. leaves some possibilities regarding its affinities. Here we compare *T. spencensis* to several taxa it might be related to.

Stalked enigmatica - *Cotyledion, Dinomischus,* and *Siphusauctum*

Tentalus spencensis has several similarities with the Cambrian genera *Dinomischus* (Fig. 3A) and *Cotyledion*. The former is known from both the middle Cambrian of North America and China (Conway Morris, 1977; Jin *et al.* 2006), while the latter is known exclusively from China (Zhang *et al.* 2013). These taxa have an elongate calyx which terminates in a crown of tentacle-like appendages. These appendages are thought to be able to move independently and are broad and flattened in morphology, similar to the tentacles of *T. spencensis*. Their position and arrangement is also similar to *T. spencensis*, appearing in lateral view as a single row of flattened petal-like structures connecting directly to and pointing away from the visceral mass. *Tentalus spencensis* also has a similarly shaped visceral cavity, although its incompleteness precludes a full description of shape.

T. spencensis has also some similarities with the stalked filter feeder *Siphusauctum* (Fig. 3B), which is known from the Burgess Shale and the Spence Shale (O'Brien & Caron 2012; Kimmig *et al.* 2017). *Siphusauctum* has a wine-glass shaped calyx which terminates in a crown of elongated feather-like appendages that move food towards the central opening.

Both *Dinomischus* and *Siphusauctum* have been considered stem-ctenophores (Zhao *et al.* 2019) and *Dinomischus* has most recently been considered a cnidarian (Ou *et al.* 2022). If these assignments are correct, and these taxa can be considered close relatives of *T. spencensis*, a deuterostome affinity would likely not be the case.

Cnidarian

Tentalus spencensis has some similarities with sessile cnidarians, such as sea anemones (Actiniaria). It appears to have a columnar trunk topped by an oral disc with a ring of tentacles and a central mouth, and the anthozoan body plan is well documented from Cambrian localities in China (Ou *et al.* 2021; Zhao *et al.* 2023; Lei *et al.* 2014). However, there is no indication that the tentacles can be retracted, nor are they as long and prehensile as those seen in Cambrian cnidarians such as *Nailiana* (Ou *et al*. 2021). The trunk shows no indication of tubercles, and while it also unclear if the stalk of *Tentalus spencensis* ends in a pedal disk or a holdfast, we see no evidence of mesentery divisions (Hou *et al.* 2005) or fine longitudinal striations (Ou e*t al.* 2021).

Ambulacrarian

A wide variety of ambulacrarian taxa are tentaculate, sessile, and have holdfasts or other benthic attachment structures, that are similar to the morphology of *Tentalus spencensis*. However, several key features, and the absence of others, make a placement within Ambulacraria problematic. First, *T. spencensis* preserves no immediate evidence of either ossicles or stereom, and is thus unlikely to represent any kind of echinoderm. This includes the possible stem-group echinoderm or stem-group ambulacrarian *Yanjiahella biscarpa* (Topper *et al.* 2019; Zamora *et al.* 2020), which is further differentiated from *T. spencensis* by having only a single pair of elongate tentacles, rather than circum-oral, broad appendages.

Another ambulacrarian group with some comparable features are the cambroernids. This includes a variety of discoidal animals such as *Eldonia*, *Stellostomites*, and *Rotadiscus*, as well as *Herpetogaster collinsi* (Fig. 3C). The latter is known from the Burgess Shale and also the slightly older Pioche and Balang formations (Caron *et al.* 2010; Kimmig *et al.* 2019b; Yang *et al.* 2024). In contrast to *T. spencensis, Herpetogaster collinsi* however has a segmented body and only two branching tentacles with dendritic extensions, rather than flattened with striations.

5.b. Other soft-bodied deuterostomes of the Spence Shale

As *Tentalus spencensis* might be a deuterostome based on the presence of tentacles, sessile lifestyle, and benthic attachment structures, as discussed above, it is worth considering the other known deuterostomes from the Spence Shale.

The first undoubted deuterostomes appear in the fossil record of Cambrian Stage 3 (Nanglu *et al.* 2023; Rahman & Zamora, 2024), and the first soft-bodied deuterostomes from Laurentia, *Herpetogaster*, are known from Cambrian Stage 4 (Kimmig *et al.* 2019b). By the Wuliuan Stage the three main deuterostome Phyla (Hemichordata, Echinodermata, Chordata) are

known from Laurentia (Kimmig *et al.* 2019a; Nanglu *et al.* 2020; Rahman & Zamora, 2024) and all of them are have been found in the Spence Shale (Kimmig *et al.* 2019a; Rahman & Zamora, 2024). In terms of soft-bodied deuterostomes four taxa are known, *Banffia episoma*, *Eldonia ludwigi*, *Sphenoecium wheelerensis* and *Yuknessia*.

Banffia episoma is the only vetulicolian known from the Spence Shale (Conway Morris *et al.* 2015a; Ma *et al.* 2025). It is relatively abundant with about a dozen specimens in museum collections, but is restricted to the shales of the Wellsville Mountain section, suggesting that it preferred deeper water environments. The most recent phylogenetic analysis (*Mussini et al., 2024*) suggests that vetulicolians are a paraphyletic group amongst stem-chordates, making *Banffia episoma* the first record of chordates in Laurentia.

Similar to *Banffia episoma*, the phylogenetically problematic *Eldonia ludwigi* (Conway Morris *et al.* 2015b ; Whitaker *et al.* 2022), currently considered a stem-ambulacrarian (Nanglu *et al.* 2023), is only found in the Wellsville Mountains, but can be highly abundant in areas, i.e., KUMIP 490969-491039 are part of large clusters of small *Eldonia ludwigi* and the KUMIP collection houses 144 specimens from the Spence Shale alone.

In terms of hemichordates, the graptolites *Sphenoecium wheelerensis* and *Yuknessia* have been described from the Spence Shale (LoDuca *et al.* 2015; Maletz & Steiner, 2015). However, while the colonial organization is verified for *Sphenoecium* (Maletz, 2024) the graptolite material assigned to *Yuknessia* requires further study. Graptolites have been found in the Wellsville Mountains and High Creek (Kimmig *et al.* 2019a; Whitaker *et al.* 2022) and are the most ecologically and geographically distributed of the soft-bodied deuterostomes in the Spence Shale.

Interestingly, no soft-bodied deuterostomes have been found in the Spence Gulch, or Blacksmith Fork locations. However, soft-tissues have been found there and Spence Gulch also preserves echinoderms (Kimmig *et al.* 2019a, 2023; Wen et al. 2019), suggesting that the conditions might have been suitable. Different taphonomic conditions (Whitaker *et al.* 2022) are most likely the reason for this, but, anthropogenic collections biases (Whitaker & Kimmig, 2020) have also led to a smaller sample size from these localities.

6. Conclusions

Although *Tentalus spencensis* gen. et. sp. nov. is very rare, its characterizing features are well preserved, such that it is possible to distinguish it from other known tentacle bearing organisms of the Cambrian. The differences lie outside the degree of biological or taphonomical variation that would be expected from organisms such as *Dinomischus*, *Siphusauctum*, or *Herpetogaster* and as such warrants the establishment of a new genus and species. In particular, the short stubby tentacles and oblong calyx shape suggests this. The occurrence of *T. spencensis* extends the diversity of the enigmatic group of early Paleozoic stalked filter feeders. The tentacles and calyx shape suggest a relationship with other Cambrian taxa, such as *Dinomischus* or possibly, but less likely early deuterostomes.

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Competing interests. The authors declare no competing interests.

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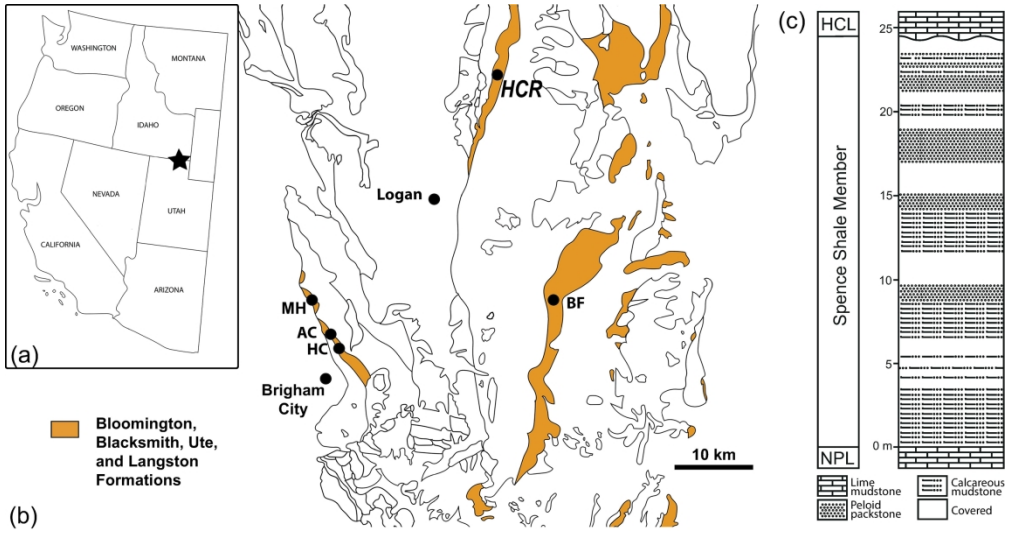
Figures

Figure 1. (Colour online) Locations of the Spence Shale Lagerstätte: (a) map of the western USA showing the location of the Spence Shale; (b) geological map (based on the USGS state maps for Google Earth Pro) of northern Utah and southern Idaho showing the principal localities within the Spence Shale; (c) simplified stratigraphy of the Langston Formation at High Creek. AC, Antimony Canyon; BF, Blacksmith Fork; HC, Hansen Canyon; HCL, High Creek Limestone Member; HCR, High Creek; MH, Miners Hollow; NPL, Naomi Peak Limestone Member.

Figure 2. (Colour online) *Tentalus spencensis* gen. et sp. nov. from the Spence Shale Member, Langston Formation (Cambrian: Wuliuan), Utah, USA. (a) SMNK-PAL 73174 laterally preserved. (b) Interpretative drawing of SMNK-PAL 73174. (c) Close-up of the preserved calyx. (d) Close-up of the partial stalk. (e) Close-up of the right tentacles preserving faint striations. (f) Close-up of the anterior part. Scale bars are 1 mm. c = calyx; pin? = putative pinnules; st = stalk; te = tentacle.

Figure 3. (Colour online) Potentially related taxa. (a) *Dinomischus isolatus* holotype from the Burgess Shale, USNM 198735. (b) *Siphusauctum lloydguntheri* holotype from the Spence Shale, KUMIP 135150. (c) *Herpetogaster collinsi* from the Pioche Formation, KUMIP 482878. (d) Close-up of the stem-calyx area of *Dinomischus isolatus* from the Burgess Shale, ROM 32573. (e) Close-up of the stem-calyx area of *Siphusauctum gregarium* from the Burgess Shale, ROM 61415. (f) Close-up of the stem-calyx area of (g) Close-up of the tentacles of *Dinomischus isolatus* from the Burgess Shale, USNM 198735. (h) Close-up of the comb segments of *Siphusauctum gregarium* from the Burgess Shale, ROM 61415. (i) Close-up of the tentacles of *Herpetogaster collinsi* from the Burgess Shale, ROM 58051. Scale bars are 5 mm (a-c, g-i), and 1 mm (d-f).



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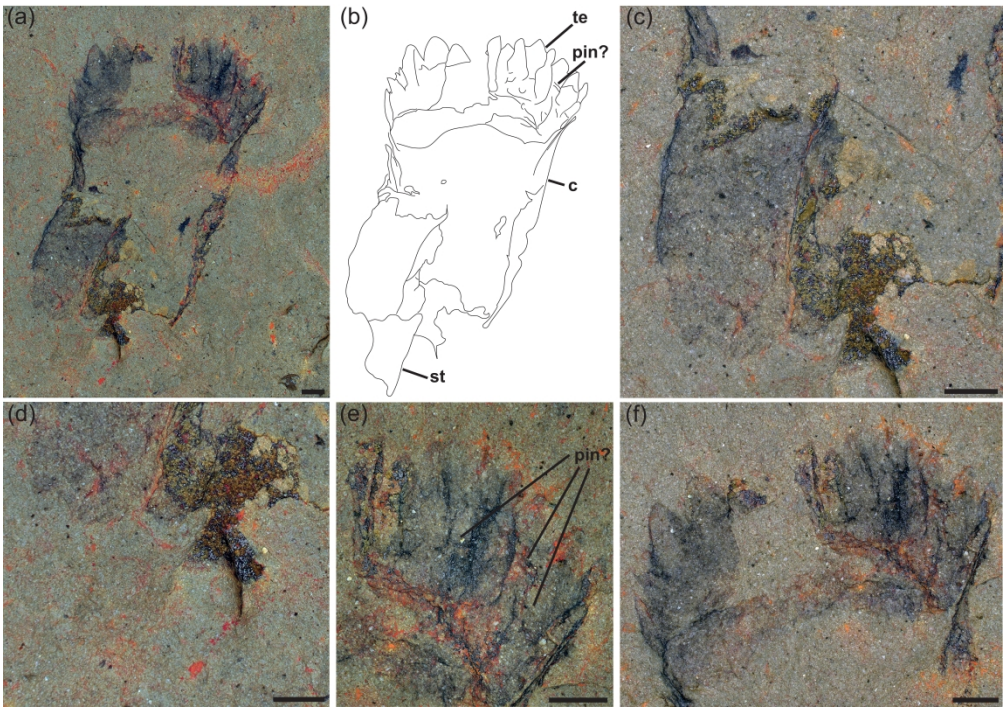

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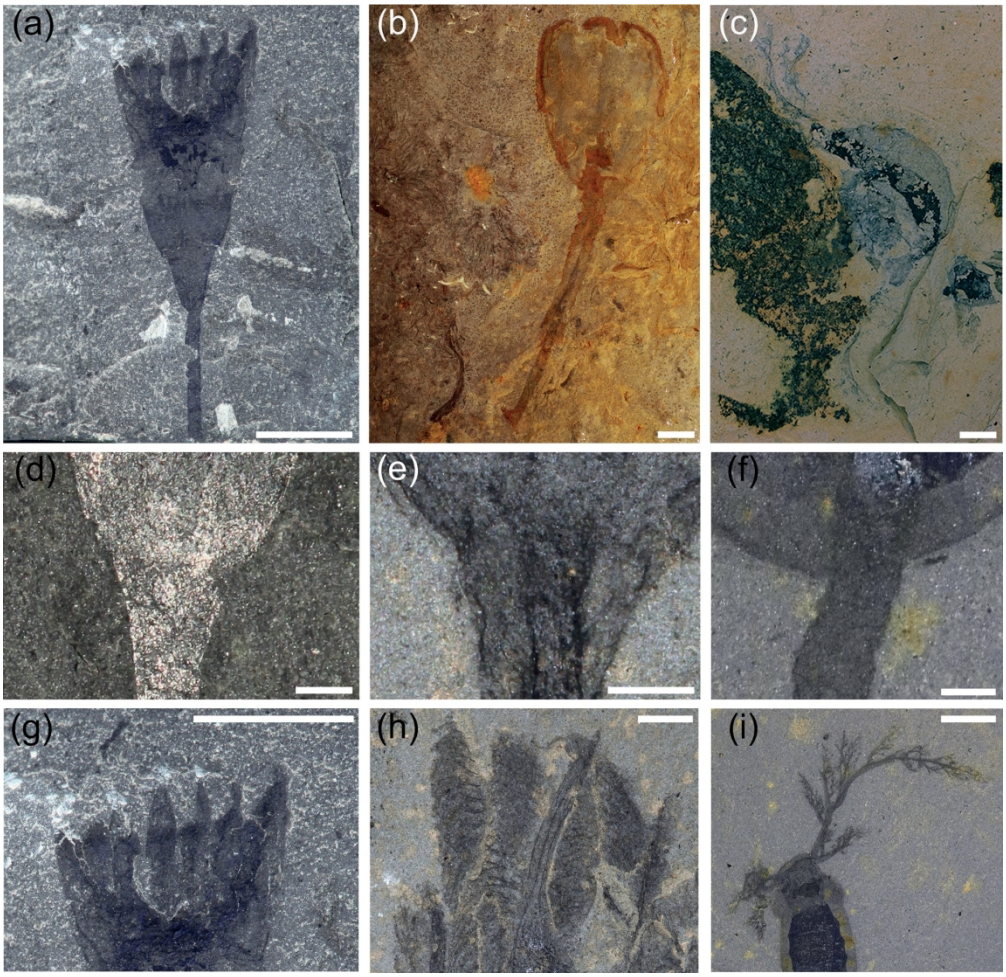

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