

The stalked filter feeder *Siphusauctum lloydguntheri* n. sp. from the middle Cambrian (Series 3, Stage 5) Spence Shale of Utah: its biological affinities and taphonomy

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Abstract.—We describe a new species of enigmatic stalked filter feeder, *Siphusauctum lloydguntheri*, from the middle Cambrian (Series 3, Stage 5) Antimony Canyon locality of the Spence Shale of northern Utah. The described specimen is the only one known from the Spence Shale, represents the first occurrence of *Siphusauctum* outside the Burgess Shale, and is only the second described species from the genus. *Siphusauctum lloydguntheri* n. sp. differs from *S. gregarium* O'Brien and Caron, 2012 in the shape of its calyx and the position of the digestive tract. The new species provides some additional information about the possible affinities of enigmatic stalked Cambrian filter feeders, as well as the taphonomic pathways that lead to preservation of *Siphusauctum*.

Introduction

Cambrian Burgess Shale-type (BST) deposits of Laurentia have proven critical for understanding the origin and evolution of the first animal communities (e.g., Briggs and Fortey, 2005; Dornbos et al., 2005; Caron and Jackson, 2008; Gaines et al., 2008; Daley et al., 2009; Edgecombe and Legg, 2013; Kimmig and Pratt, 2015; O'Brien and Caron, 2015). The middle Cambrian (Series 3, Stage 5) Spence Shale Member of the Langston Formation is one such deposit, containing a diverse array of soft-bodied taxa, trilobites, and other shelly organisms (e.g., Briggs et al., 2008; Gaines et al., 2008, 2012; Brett et al., 2009; Halgedahl et al., 2009). Discoveries from this unit have provided useful insights into the phylogeny, ecology, and biogeography of Cambrian life (e.g., Hendricks and Lieberman, 2008; Hendricks et al., 2008; Robison and Babcock, 2011; Stein et al., 2011; Daley et al., 2013; Conway Morris et al., 2015; LoDuca et al., 2015). Some of the most obscure taxa found in BST deposits are stalked filter feeders. Several species of these have been described from the Burgess Shale (e.g., *Dinomischus isolatus* Conway Morris, 1977; *Lyracystis radiata* Sprinkle, 1973; *Priscansermarinus barnetti* Collins and Rudkin, 1981; and *Siphusauctum gregarium* O'Brien and Caron, 2012). Others have been described from the Chengjiang biota (e.g., *Dinomischus venustus* Chen, Hou, and Hao-Zhi, 1989; *Phlogites longus* Luo and Hu in Luo et al., 1999; and *Cotyledion tylodes* Luo and Hu in Luo et al., 1999), and Kaili biotas (e.g., *Dinomischus* sp. Peng et al., 2006). These taxa clearly represent a polyphyletic assemblage. Some have been identified as arthropods (e.g., *P. barnetti*, Collins and Rudkin, 1981), whereas others are interpreted to be echinoderms (e.g., *L. radiata*, Sprinkle, 1973). *Phlogites longus* is treated as a

primitive deuterostome (Caron et al., 2010) and *Dinomischus* and *Cotyledion* may be entoprocts (Conway Morris, 1977 and Zhang et al., 2013, respectively). The affinities of *Siphusauctum* are, at present, indeterminate (O'Brien and Caron, 2012).

We describe a new species of stalked filter feeder, *Siphusauctum lloydguntheri*, from the Spence Shale that extends the geographic range of this genus to southern Laurentia. The anatomy of the stem of the Spence Shale species is closely comparable to that of the slightly younger *S. gregarium*, which is known from the Tulip Beds of the Cliff Shale Member of the Burgess Shale Formation (Fletcher and Collins, 2003; O'Brien and Caron, 2012). However, the crown calyx of *S. lloydguntheri* differs in shape, the positioning of some of the interior organs, and the arrangement of the filter feeding apparatus, relative to *S. gregarium*. Our examination of this new species of *Siphusauctum* provides some insight into the affinities of this enigmatic taxon.

Geological setting

The Spence Shale Member is part of the Langston Formation, which is a regionally extensive, relatively deep-water middle Cambrian (Series 3, Stage 5) unit in northern Utah and southern Idaho (Fig. 1; Liddell et al., 1997) that ranges in age from the *Albertella* to *Glossopleura* biozones (Liddell et al., 1997; Robison and Babcock, 2011). The Burgess Shale, by contrast, is slightly younger (*Bathyuriscus–Elrathina* biozones), but shares several taxa in common with the Spence Shale Member (*Glossopleura* Biozone; Briggs et al., 2008; Hendricks et al., 2008; Conway Morris et al., 2015; LoDuca et al., 2015). It was deposited on the passive western margin of Laurentia. The Spence Shale Member is one of four middle Cambrian Burgess

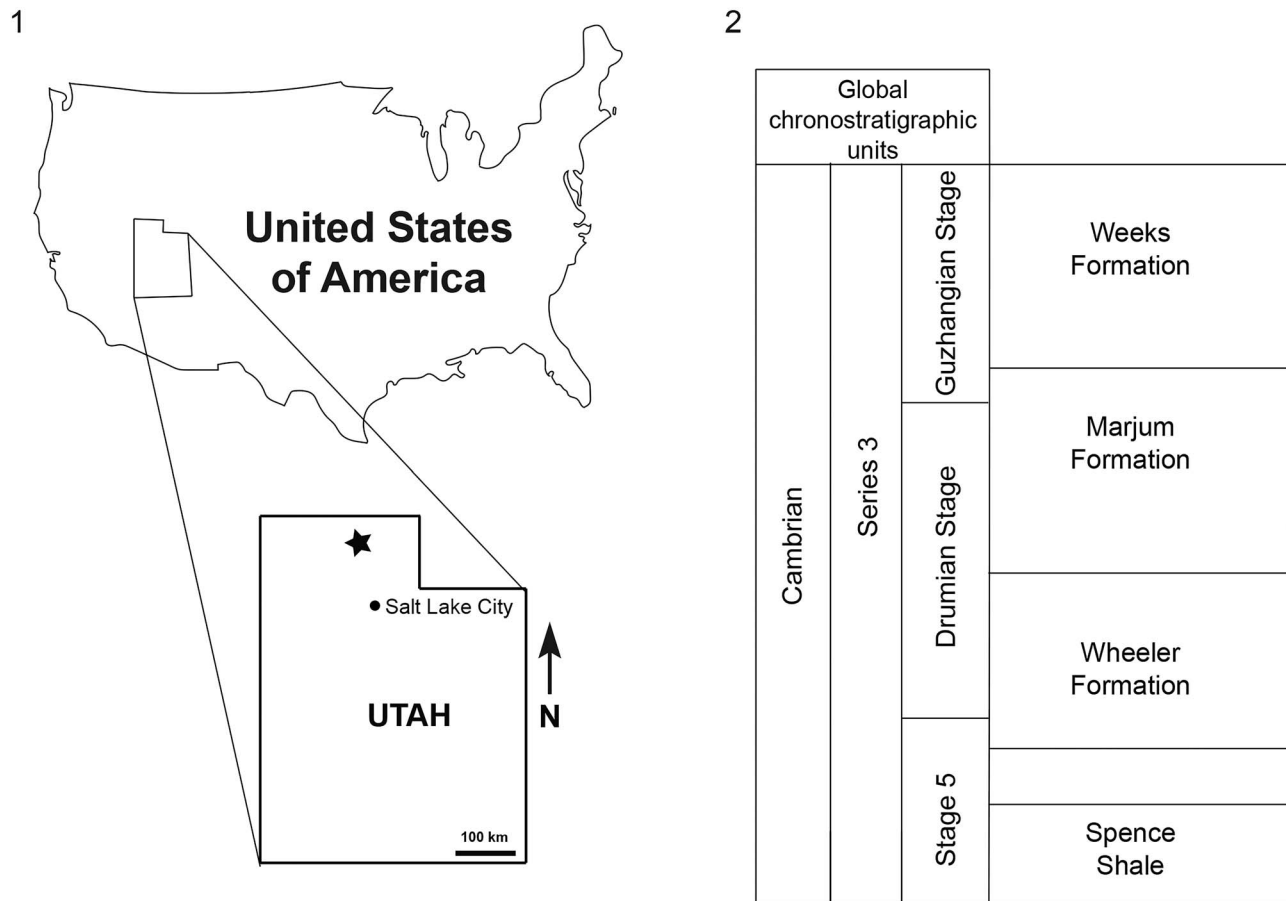


Figure 1. (1) Location of the Spence Shale locality (asterisk; 41.561 N, 112.006 W), Antimony Canyon, Box Elder Co., Utah; (2) Generalized stratigraphic correlation of the major middle Cambrian Burgess Shale-type deposits in Utah.

Shale-type deposits that occur in Utah (Robison and Babcock, 2011). Paleogeographically, it was part of the fine-grained middle carbonate or outer detrital belt of the eastern Great Basin that was probably seaward of a carbonate platform that subsequently planed off (Robison, 1991; Liddell et al., 1997). The presence of certain types of trace fossils indicates dynamic redox conditions during deposition (Garson et al., 2012).

The specimen we describe was found on a silty shale float slab ~5 m below the top of the Spence Shale Member on the south side of Antimony Canyon, which is situated on the west flank of the Wellsville Mountains north of Brigham City, UT (41.561 N, 112.006 W). The Spence Shale in this area is ~64 m thick and consists of a succession of shales, silty shales, lime mudstones, wackestones, and packstones that lies above the Naomi Peak Limestone Member and beneath the High Creek Limestone Member (Liddell et al., 1997). By contrast, to the north, the Spence Shale is overlain by thin-bedded silty and sandy limestones of the Ute Formation (Chappelle, 1975; Liddell et al., 1997).

Materials and methods

The specimen was photographed using a Canon EOS 5D Mark II digital SLR camera equipped with Canon 50 mm macro lens. Pictures were taken with specimens submerged in alcohol. The contrast, color, and brightness of images were adjusted using

Adobe Photoshop. Line drawings were created in Adobe Illustrator.

Repositories and institutional abbreviations.—The part and counterpart of the specimen were collected and donated by Lloyd Gunther in 1976 and are housed in the collections of the Division of Invertebrate Paleontology, Biodiversity Institute, University of Kansas (KUMIP). Specimens with the prefix ROM are housed in the Royal Ontario Museum, Ontario, Canada.

Systematic paleontology

Morphological terminology follows O'Brien and Caron (2012).

Unranked stem-group bilaterian

Remarks.—O'Brien and Caron (2012) identified *Siphusauctum gregrium* as an unranked stem-group bilaterian. The new species described herein unfortunately does not offer any further insight into the higher-level taxonomy of the genus, and thus we leave this open to further study.

Phylum, Class, Order Uncertain
Family Siphusauctidae O'Brien and Caron, 2012

Remarks.—O'Brien and Caron (2012) discussed the possibility that *Dinomischus* could be closely related to *Siphusauctum*, but concluded that finding homologous characters between the two genera was difficult, given the limited availability of *Dinomischus* specimens. We follow this conclusion and do not include *Siphusauctum* in the family Dinomischidae (see Conway Morris, 1977 for more discussion of this taxon).

Genus *Siphusauctum* O'Brien and Caron, 2012

Type species.—*Siphusauctum gregarium* O'Brien and Caron, 2012.

Diagnosis.—Soft-bodied, gregarious, stalked, upright metazoan, divided into three distinct parts from top to bottom: a prominent, chalice-shaped calyx; this is attached to a narrow stem; the stem terminates in a small, bulbous or flat holdfast rarely wider than the stem. Maximum dimensions 223 mm high and 48 mm wide (at calyx). Calyx box-shaped to oblate, approximately circular in cross-section with a rigid conical lower quarter attached to stem. Maximal width at mid-height of narrow ridge, width tapering or constant towards top. Calyx covered with thin external sheath representing margins of possible filtration chamber. External sheath smooth and unbroken, with exception of small openings at base of calyx; an opening for anus at top, with indistinct openings around anus, and possible openings on protrusions half way up calyx. Internal structures include central and prominent sac-like gut enclosed by tube representing margins of body cavity. Gut is differentiated into three main zones: ovoid lower tract near base of calyx; this grades into bulbous mid-gut; then tapers into straight and thin upper intestine projecting upwards to central terminal anus. Gut enclosed within body cavity surrounded by hexaradial filter-feeding segments arranged longitudinally and filling most of calyx. Outer surface of each segment consists of fine, diagonally oriented, parallel striae. Internally, pair of thick transverse comb-like grooves (>30? pairs per segment) occupies most of width and height of segments. Grooves taper to thin point towards body cavity and connect to larger groove extending from top of calyx to level of lower gut along outer edge of segments. Stem flexible but generally straight; of uniform width, and divided into inner and outer layer. Length (sag.) of stem one to three times length of calyx (modified from O'Brien and Caron, 2012, based on new information provided by *S. lloydguntheri* n. sp.).

Occurrence.—Tulip beds locality (see O'Brien and Caron, 2012), Campsite Cliff Shale Member, Burgess Shale Formation on Mount Stephen, British Columbia, Canada, middle Cambrian, Series 3, Stage 5, lowermost *Bathyuriscus* Biozone; and Langston Formation, Spence Shale Member, Antimony Canyon area, west flank of the Wellsville Mountains, Utah, (41.561 N, 112.006 W), middle Cambrian, Series 3, Stage 5, *Glossopleura* Biozone.

Remarks.—The new species from the Spence Shale possesses the diagnostic characteristics of the genus, including directly comparable stem and holdfast structures, the placement of the digestive tract in the lower part of the calyx, the presence of sheath protrusions in the outer wall of the calyx, the placement of the anus, and the shape of the upper part of the calyx.

Siphusauctum lloydguntheri new species

Figures 2.1, 2.2, 3.1–3.4, 4.1–4.4

2012 *Siphusauctum* sp.; O'Brien and Caron, p. 6.

Holotype.—KUMIP 135150, one laterally compressed specimen, preserved as both part and counterpart.

Diagnosis.—Soft-bodied stalked metazoan with chalice-like body, obovate calyx with thickened external sheath, pair of small lateral protrusions half way up calyx, narrow internal stem mantled by outer stem, and flattened holdfast growing out of inner stem at base. Stem-length to calyx-length ratio 1.3:1.

Occurrence.—Langston Formation, Spence Shale Member, Antimony Canyon area, west flank of the Wellsville Mountains, Utah, (41.561 N, 112.006 W), middle Cambrian, Series 3, Stage 5, *Glossopleura* Biozone.

Description.—The specimen is laterally compressed and composed of an obovate calyx-like upper part, with maximum length 35.1 mm and maximum width 25.9 mm, and a slim stem, which is 45.6 mm long, has a maximum width of 5.5 mm, and ends in a flattened basal holdfast that is 5.7 mm wide and 0.9 mm high.

The stem is composed of an inner and outer stem (Fig. 4.1–4.4). The slender inner stem terminates in the holdfast and extends upward at least into the base of the calyx, perhaps slightly higher, is 2.4 mm wide just above the holdfast, reaches a minimum width of 1.5 mm near the center of the stem, and has width of 1.7 mm at the base of the calyx. The outer stem is preserved from the base of the calyx to ~16.8 mm above the holdfast. It appears to have continued past the point of preservation and likely extended all the way to the holdfast. Where the outer stem is preserved, it has a width of ~5.5 mm and appears to have mantled the inner stem. The outer stem has wrinkles or grooves near the base of the calyx, but is smooth from 10 mm beneath the calyx to the limits of preservation. The inner and outer stem were likely made of different tissues, because the inner stem has a greater preservation potential than the outer stem. The holdfast appears to be a direct continuation of the inner stem, and was likely made of the same tissue. It is 5.7 mm wide and 0.9 mm high.

The stem smoothly extends into the conical base of the calyx (Fig. 3.1–3.4) and through the bottom 15.9 mm of the calyx, which is approximately half way up the calyx, roughly opposite a pair of small lateral protrusions from the calyx outer wall. The angle between the outer wall of the calyx and the stem is ~125°. Because the outer stem is preserved in the same way as the lower part of the calyx, it suggests that the calyx and the stem may have formed a continuous functional unit. There is a direct connection between the carbonaceous part of the stem that is preserved at the base of the calyx and the ovoid structure above it, which likely represents part of the digestive tract.

The obovate calyx seems to have been covered by a thick, likely compressed, outer sheath. Half way up the outer sheath of the calyx, the specimen has small (0.8 mm) protrusions present on both sides of the calyx; each protrusion could be an opening in the calyx, as it is not preserved as prominently as the



Figure 2. Holotype of *Siphusauctum lloydguntheri* n. sp. (KUMIP 135150) from the Spence Shale, middle Cambrian, Antimony Canyon, Utah, in lateral view: (1) part; (2) counterpart. Scale bar represents 10 mm.

surrounding outer sheath of the calyx. The only interior parts of the calyx preserved are two basal, dark, carbonaceous structures, connected by a small piece of tissue. These are interpreted as part of the lower digestive tract. The upper structure is relatively elongate, ~5.7 mm wide by 6.5 mm long; the lower structure is nearly square, ~5.7 mm by 5.7 mm.

The calyx has fine, elongate carbonaceous structures that start about half way up the calyx and end at the outer sheath at the top of the calyx. These are inferred to be comb segments, although no transverse grooves or striae are preserved. Alternatively, they might represent openings into the interior of the calyx, where a possibly fixed filter apparatus might have been located.

Two grooves are preserved near the top of the calyx. These grooves are 6.9 mm and 8.5 mm away from the edge of the calyx and may indicate the location of the anus.

Etymology.—After Lloyd Gunther, who collected and donated the specimen.

Remarks.—*Siphusauctum lloydguntheri* n. sp. differs from *S. gregarium* by having an obovate calyx, as opposed to an orbicular calyx. In particular, in *S. lloydguntheri* the calyx projects at a larger angle, as measured upwards from the stem, and is slimmer, relative to *S. gregarium*. Although aspects of

these features could vary with degree of preservation and angle to bedding plane, the fact that so many specimens of *S. gregarium* examined by O'Brien and Caron (2012) do not exhibit these characteristics suggests some underlying biological differences. The lower digestive tract is also closer to the base of the calyx than in *S. gregarium*. While thin structures indicating grooves or the upper digestive tract are present in *S. lloydguntheri* n. sp., there is no indication of transverse grooves, striae, or comb segments. This is different from the condition in *S. gregarium*. It may be that these were simply not preserved, or perhaps the filter itself and the overlying external sheath of the calyx were more rigid in *S. lloydguntheri* n. sp. The differences identified between the two species have been used to amend the genus-level diagnosis. It might be that some of the differences are a result of taphonomic artifact, rather than representing actual biological differences, but the copious material of *S. gregarium* studied by O'Brien and Caron (2012) does not appear to show these features.

Discussion

Life mode and biologic affinities.—It is difficult to determine the mode of life for *S. lloydguntheri* n. sp. because only one specimen is known. It is likely that, like *S. gregarium*, it was a sessile

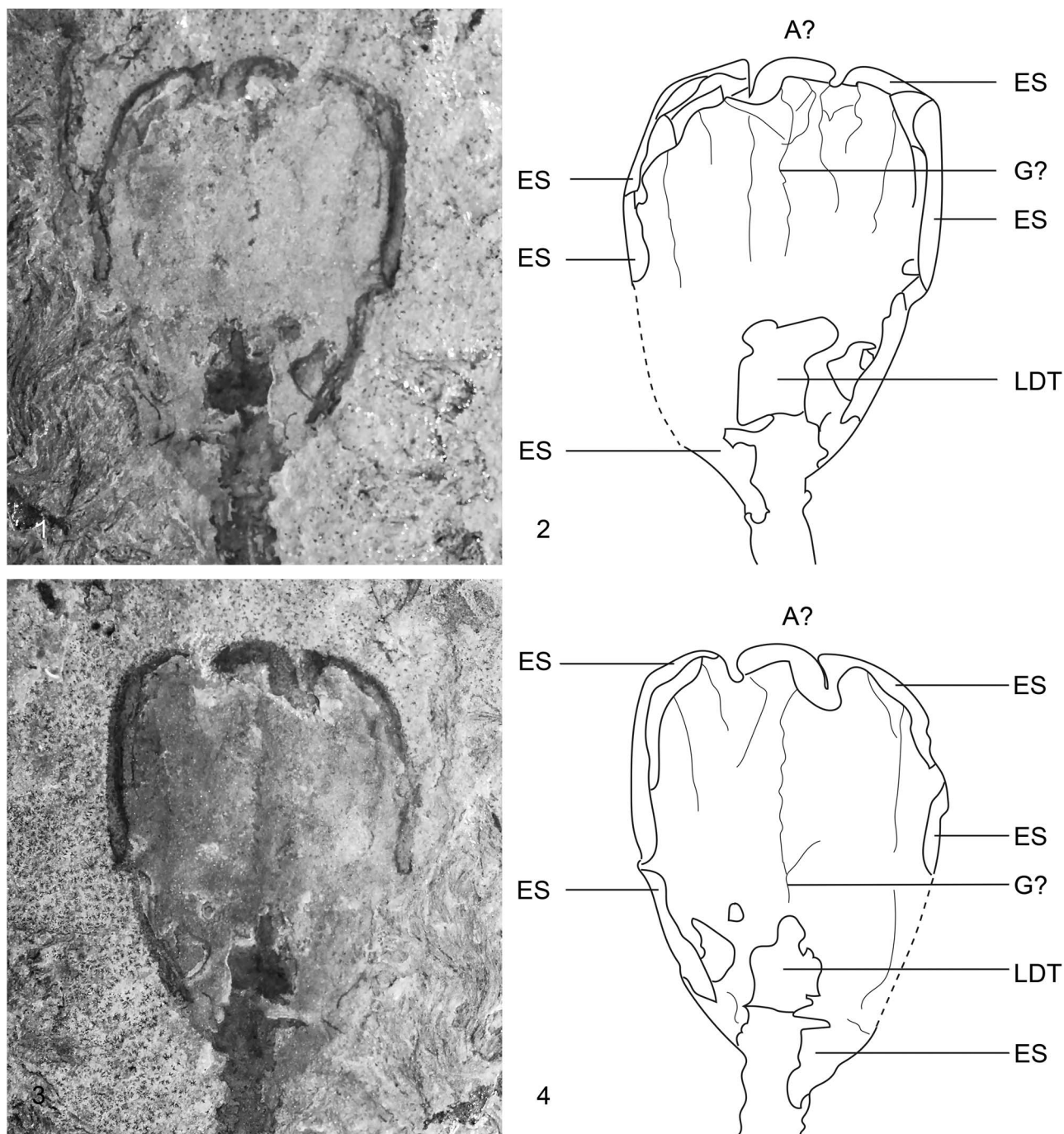


Figure 3. Close-up of the calyx of the holotype of *Siphusauctum lloydguntheri* n. sp. (KUMIP 135150) from the Spence Shale, middle Cambrian, Antimony Canyon, Utah: (1) part; (2) explanatory drawing of the part, dashed line indicates uncertain outline; (3) counterpart; (4) explanatory drawing of the counterpart, dashed line indicates uncertain outline. Scale bar represents 5 mm. Abbreviations: A = Anus, ES = External Sheath, LDT = Lower digestive tract, G = Gut.

to semi-sessile animal and anchored itself in the soft sediment. If it was semi-sessile, the holdfast was likely retractable, as assumed for *S. gregarium* (O'Brien and Caron, 2012), but more specimens are needed to confirm this assumption. *Siphusauctum lloydguntheri* n. sp. would have likely moved with bottom currents because there are no apparent body parts to indicate it was an active swimmer. While *S. gregarium* was a gregarious animal, only one specimen of *S. lloydguntheri* n. sp. is known from the Spence Shale. This might be a result of transportation

of the specimen to its burial place, or could perhaps indicate a more solitary mode of life. The presence of well-preserved planktonic algae buried alongside *S. lloydguntheri* n. sp. and several specimens of *S. gregarium*, as well as the exposed holdfast, suggest some minor transportation took place. O'Brien and Caron (2012) mentioned that no budding polyps have been observed on the stem or calyx of *S. gregarium*, and *S. lloydguntheri* n. sp. does not preserve any evidence of budding either, although this might be a taphonomic bias.

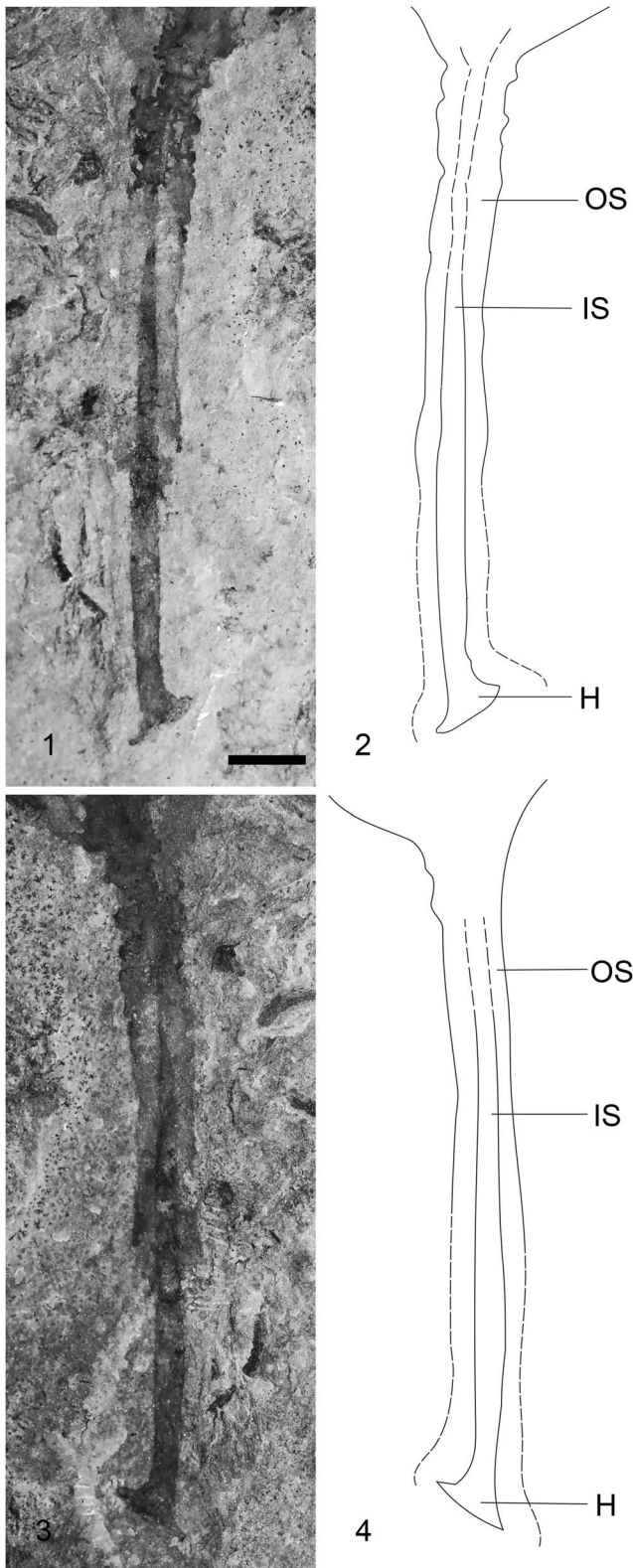


Figure 4. Close-up of the stem of the holotype of *Siphusauctum lloydguntheri* n. sp. (KUMIP 135150) from the Spence Shale, middle Cambrian, Antimony Canyon, Utah: (1) part; (2) explanatory drawing of the part, dashed line indicates uncertain outline; (3) counterpart; (4) explanatory drawing of the counterpart, dashed line indicates uncertain outline. Scale bar represents 5 mm. Abbreviations: H = Holdfast, IS = Inner Stem, OS = Outer Stem.

O'Brien and Caron (2012) compared *Siphusauctum gregarium* with several other stalked organisms and did not uncover any close relatives among extinct or extant animals. Reevaluating this information, and given that *S. lloydguntheri* n. sp. differs in some respects from *S. gregarium*, thereby providing some new information on the morphology of *Siphusauctum*, the potential affinities of the taxon are worth reconsidering. In particular, the absent prominent comb segments of *S. lloydguntheri*, if a true absence, suggests possible affinity with *Dinomischus isolatus*. These might be the shared plesiomorphic condition, with the comb segments acquired in *S. gregarium*. The calyx of *Siphusauctum lloydguntheri* n. sp. has an obovate outline similar to that of the crown of *D. isolatus*, and both have the digestive tract or stomach closer to the base of the calyx than *S. gregarium*. However, *Siphusauctum lloydguntheri* n. sp. lacks several characteristic features of *Dinomischus*, including the bracts and the very long stem lacking a distinction between inner and outer parts (see Conway Morris, 1977; Chen et al., 1989). Thus, a direct sister group relationship between the two is not indicated. Conway Morris (1977) suggested that *Dinomischus* possesses characteristics of entoprocts, a minute, extant, "pseudocoelomate" grade phylum, which is an interpretation challenged by Todd and Taylor (1992). If Conway Morris' (1977) interpretation ultimately is vindicated, given the commonalities of the two taxa, this would suggest a potential link to entoprocts for *Siphusauctum* as well. Entoprocts possess six-fold symmetry in the crown or calyx, which both *Dinomischus* and *Siphusauctum* also have: a shared feature not previously identified (Conway Morris, 1977; O'Brien and Caron, 2012). Given that symmetry patterns characterize several higher taxa (e.g., Echinodermata), and six-fold symmetry can otherwise only be found in some cnidarians (e.g., Hexacorallia), this is potentially strong evidence for treating both *Dinomischus* and *Siphusauctum* as stem-group entoprocts. However, further direct comparisons among *Siphusauctum*, *Dinomischus*, and modern entoprocts are at present difficult, due to the minute size of the latter. Some previous comparisons of BST organisms have suggested affinities with modern groups that differ substantially in size. For example, Lieberman (2008) described how taxa known from Burgess Shale-type deposits that reached substantial body size, such as vetulicolians, share certain traits in common with minute extant "pseudocoelomate" grade organisms, such as kinorhynchs. Zhang et al. (2013) identified a similar phenomenon when they favorably compared the macroscopic early Cambrian *Cotyledion* from the Chengjiang biota with entoprocts. Unfortunately, the tentacles ringing the margin of the calyx are not completely preserved in *Cotyledion* (Zhang et al., 2013). Because the precise number of tentacles could not be determined, although Zhang et al. (2013) estimated there is space for approximately 34 of them, it is impossible to verify whether six-fold symmetry is also seen in this putative stem entoproct. *Cotyledion* does differ from *Siphusauctum* in several respects. The former appears to be covered with sclerites, and seems to lack the pronounced distinction between inner and outer stems, although this could be present but obscured by what Zhang et al. (2013) interpreted as a covering of sclerites. However, they both possess a tri-partite body plan, and the overall shape of the calyx is similar, along with the

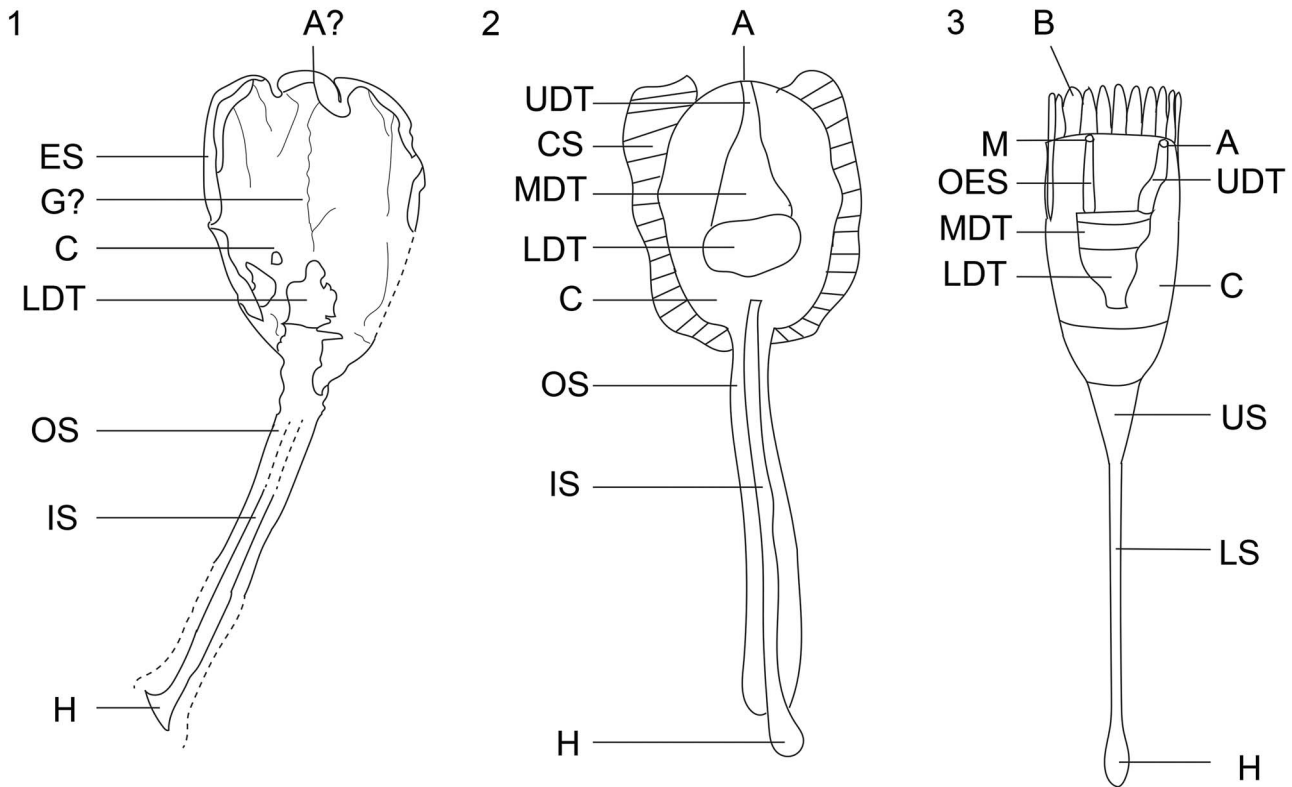


Figure 5. Comparison of three species of stalked filter feeders: (1) *Siphusauctum lloydguntheri* n. sp.; (2) *Siphusauctum gregarium*; (3) *Dinomischus isolatus*. Abbreviations: A = Anus, B = Bract, C = Calyx, CS = Comb Segments, ES = External Sheath, G = Gut, H = Holdfast, IS = Inner Stem, LDT = Lower digestive tract, LS = Lower Stem, M = Mouth, MDT = Middle Digestive Tract, OES = Oesophagus, OS = Outer Stem, UDT = Upper Digestive Tract, US = Upper Stem.

position of the anus. Apart from the seemingly superficial fact that *Siphusauctum* is organized into a stem and calyx, there appears to be few homologous features shared by it and various Cambrian echinoderms, including *Lyracystis*, *Gogia*, and *Castericystis* (Sprinkle, 1973; Ubaghs and Robison, 1988; Sprinkle and Collins, 2006; Zamora and Smith, 2012). However, it is apparent from the Tulip beds locality, as well as the Spence Shale, that echinoderms and *Siphusauctum* inhabited the same, or similar, habitats, because they co-occur in both deposits (Sprinkle, 1973; O'Brien et al., 2014).

Taphonomy and ecological associations.—*Siphusauctum gregarium* is extraordinarily abundant in the Tulip beds of Mount Stephen (at least 1,525 specimens), but has not been reported from the Phyllopod bed of the Burgess Shale or the Marble Canyon locality (Caron et al., 2014; O'Brien and Caron, 2015), even though these localities contain very species-rich Burgess Shale-type deposits. The mass preservation of specimens in the Tulip beds at present appears to be a singular event, and suggests that the *Siphusauctum* body might have been less likely to be preserved under the conditions that led to Burgess Shale-type preservation at most localities. This may explain why, after years of excavations in the Spence Shale Member, only one specimen of *Siphusauctum* has been found. Interestingly, *Siphusauctum* co-occurs in both the Tulip beds and the Spence Shale with specimens of the algae *Marpolia* (Fig. 2.1, 2.2; O'Brien and Caron, 2012: ROM 61415, fig. 4; ROM 61417, fig. 5B; ROM 61420, fig. 6A). *Marpolia* was likely a planktonic alga (personal communication, S. LoDuca, 2016), which

might indicate that the specimen described herein was transported by currents. Thus, it did not necessarily live on the silica-rich substrate where it was preserved. This interpretation is also supported by the exposed holdfast, which in life would have been buried. If transport did occur, it was likely not via turbidity currents or strong storms because the delicate, soft-bodied *S. lloydguntheri* n. sp. would be unlikely to survive the associated forces.

Full preservation of the external sheath, the inner stem, and most of the outer stem, as well as parts of the digestive tract and interior calyx structure, indicates a low degree of degradation (Wilson and Butterfield, 2014; Kimmig and Pratt, 2016; Naimark et al., 2016). The associated *Marpolia* specimens (Fig. 2.1, 2.2) are also well preserved. Because the internal elements of *S. gregarium* decayed more slowly than the external sheath (O'Brien and Caron, 2012), there are three explanations for the missing comb segments of *S. lloydguntheri* n. sp. The first possibility is that *S. lloydguntheri* n. sp. did not actually have comb segments, and the faintly preserved carbonaceous structures represent a somewhat different filtering system from *S. gregarium*. This possibility seems rather unlikely given the other profound similarities between *S. lloydguntheri* n. sp. and *S. gregarium*. The second possibility is that the preservation pathway in the Spence Shale preferably preserved the external tissues of the specimen, and for chemical or biological reasons did not preserve the comb segments. The third possibility is that the specimen lost its comb segments through transport or scavenging. Unfortunately, no evidence currently exists to differentiate among these three possibilities, but resolving the

presence or absence of comb segments in *S. lloydguntheri* n. sp. is a vital step towards resolving the taxonomic affinities of the genus and determining if *Siphusauctum* is a stem-group entoproct.

Conclusions

Although *S. lloydguntheri* n. sp. is very rare, its counterpart *S. gregarium* has been extremely well characterized, such that it is possible to distinguish the former as lying outside the degree of biological or taphonomical variation shown in the latter. In particular, the different calyx shape, placement of the digestive tract, and the interior calyx structure suggest that separating these two species is warranted. The occurrence of *Siphusauctum* in the Spence Shale extends its geographic range into the Great Basin, and slightly expands the temporal range for this enigmatic group of early Paleozoic stalked filter feeders. Certain characteristics of *S. lloydguntheri* n. sp. might suggest a relationship with other Cambrian taxa, such as *Dinomischus* and *Cotyledion*, and possibly with modern entoprocts.

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