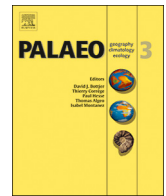




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Paleobiology of a three-dimensionally preserved paropsonemid from the Devonian of New York

James W. Hagadorn^{a,*}, Warren D. Allmon^b^a Department of Earth Sciences, Denver Museum of Nature and Science, Denver, CO 80205, USA^b Paleontological Research Institution, Department of Earth and Atmospheric Sciences, Cornell University, 1259 Trumansburg Road, Ithaca, NY 14850, USA

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ABSTRACT

A three-dimensionally preserved stellate fossil from the Middle-Upper Devonian of New York is described. Although it shares gross similarities with oral cones of anomalocaridids, we interpret it as the mold of the dorsal portion of the segmented alimentary canal of the rare, soft-bodied animal *Paropsonema cryptophya*. Together with two other dorsally preserved *P. cryptophya* specimens, such fossils strengthen the hypothesized link between two primitive deuterostome stem groups - the paropsonemids and the eldonids. Although the taxonomic affinities of these groups remain uncertain, it is important to illustrate fossils like these because they provide paleontologists with a 'search image' for more material that may elucidate patterns in early animal evolution or may help revise taxonomic interpretations. The new specimen of *Paropsonema* is also the youngest described occurrence of the paropsonemids and its sediment-filled gut is consistent with an epibenthic lifestyle for that group.

1. Introduction

Stellate to discoidal soft-bodied fossils such as scyphomedusae or "Peytoia" are extremely rare, but when interpreted with adequate taxonomic context, they can provide insights into the paleobiology of soft-bodied animals that are rarely preserved. Unfortunately, it is difficult to interpret such fossils because they are usually only known from single or few specimens, and because they are preserved in unusual manners (Häntzschel, 1970). For example, compare discoidal medusa fossils described by Haeckel (1866) to discoidal arthropod mouths interpreted as medusae by Walcott (1898, 1911).

Ordovician and Devonian strata of New York contain these types of fossils. They include morphologically similar stellate, discoidal, and radial fossils that have had a long and varied history of interpretation, including as corals (*Discophyllum peltatum*; Hall, 1847); porpitoïd hydrozoans (e.g., *Paropsonema cryptophya*; Ruedemann, 1916; Caster, 1945; Stanley Jr., 1986); scyphozoans (Chapman, 1926); echinoids (Clarke, 1900); lophophorates (Sun and Hou, 1987; Dzik et al., 1997) and stem-group echinoderms (Conway Morris, 1993; Friend, 1995). Morphologically similar fossils also occur in coeval strata of England, including *Actinophyllum spinosum* (Barrois, 1891; Straw, 1926) and *Pseudodiscophyllum windermereensis* (Fryer and Stanley Jr., 2004), interpreted as calcareous algae and porpitoïds, respectively. All of these fossils are only known from a few specimens and many have only been

recorded from only one locality—in stark contrast to deposits that bear thousands of discoidal soft-bodied fossils like the Tafiltal or Elk Mound Konservat-Lagerstätten (Samuelsson et al., 2001; Hagadorn et al., 2002).

Here we describe another enigmatic stellate fossil from New York, compare it to previously known specimens, and suggest its affinity with *Paropsonema cryptophya* Clarke, 1900. The specimen was previously examined by Friend (1995), but most of his work remains unpublished (Friend et al., 2002). The specimen described here is noteworthy not only because it is one of only two paropsonemids from New York to come to light in almost a century, but when combined with two other dorsally preserved *Paropsonema* specimens, it reinforces the established link between *Paropsonema* and the more common discoidal animal *Eldonia* (Durham, 1974; Sun and Hou, 1987; Conway Morris and Robison, 1988; Conway Morris, 1993; Chen et al., 1995; Friend, 1995; Friend et al., 2002; Zhu et al., 2002; Ivantsov et al., 2005; Van Roy, 2006; Johnston et al., 2009; MacGabhann, 2012; MacGabhann and Murray, accepted). *Eldonia*, *Paropsonema*, and several other eldonids (discussed below) are all two-dimensionally preserved discoidal soft-bodied animals that share a segmented coiled to u-shaped alimentary tract that is occasionally sediment-filled and preserved in three dimensions like a sac. Together, they are part of a clade that may have affinities with pterobranch hemichordates and primitive pre-radial echinoderms (Friend, 1995; Caron et al., 2010; MacGabhann, 2012).

* Corresponding author.

E-mail address: jwhagadorn@dmns.org (J.W. Hagadorn).<https://doi.org/10.1016/j.palaeo.2018.08.007>

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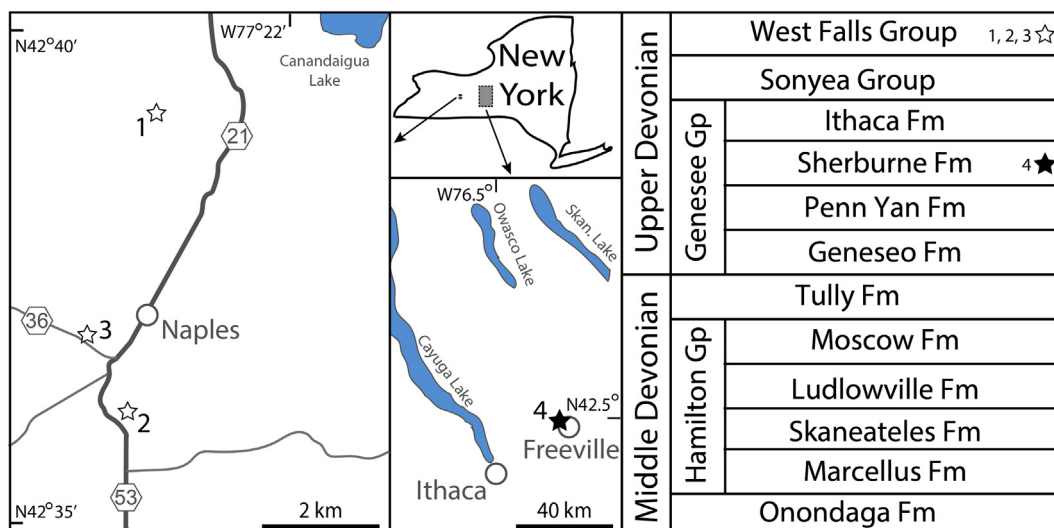


Fig. 1. Stratigraphic and geographic context for paraprosonemid specimens and localities discussed in the text. Localities include West Hill (1), Tannery Gully (2), Johnson's Glen (3), and Freeville (4), New York. Grey shaded areas are the Finger Lakes.

2. Geologic context

The first specimen, repositated at the Paleontological Research Institution (PRI), was collected from float in 1991 by an avocational paleontologist and PRI volunteer, Eleanor Bayley, near her home in Freeville, near Ithaca, Tompkins County, New York. Its precise stratigraphic provenance is uncertain. In this region, strata of the upper Hamilton Group (Moscow Shale) and the lower Genesee Group (Genesee, Penn Yan, Sherburne, Ithaca formations) are well exposed (Fig. 1; Fisher et al., 1970). Locally, exposures of these strata represent subtidal to deeper marine facies (Bartholomew and Brett, 2007). Thus, although the exact stratigraphic position from which this specimen (PRI 42122) was collected is not known, it is possible to constrain its provenance to a Middle-Upper Devonian subtidal marine setting. The specimen occurs in a very fine-grained laminated quartz wackestone, and is preserved in convex hyporelief as a ferruginous (?hematitic) cast filled with aluminosilicate (clay) and siliceous (quartz) minerals. The matrix lithology, and its grey color, is similar to strata of the Sherburne Formation, a unit that is exposed near Freeville.

Comparable material of *Paropsonema cryptophya*, including the specimen figured here (Fig. 2A–D), was collected at the turn of the 20th century by D. Dana Luther and Charles Baker (Ruedemann, 1916; Chadwick, 1923) at three outcrops to the west of Lake Canandaigua (Tannery Gully, West Hill, Johnson's Glen, Ontario County, NY). The stratigraphic provenance of these float-collected specimens (now in the collections of the New York State Museum, NYSM) is also problematic, because stratigraphic nomenclature used at the time (e.g., “Portage Beds”, “Chemung Beds”, “Hatch Formation”) actually corresponds to facies which repeat through several transgressive-regressive cycles in the Paleozoic marine succession of western New York (Isachsen et al., 1992; Bartholomew and Brett, 2007). In the area where these specimens of *P. cryptophya* were collected, units of the Upper Devonian West Falls Group (Clarke and Luther, 1904); similar paropsonemids in the collection of the New York State Museum (NYSM; discussed below) are also thought to come from the Grimes Siltstone, a unit of the West Falls Group (MacGabhann, 2012). Most of the material collected from these outcrops consists of thinly interbedded micaceous fine- to very-fine grained sandstones interbedded with black to grey mudstones. Fossil-bearing slabs in the NYSM commonly bear load casts and runzelmarken on bed interfaces and fossils are preserved on bed tops and bed soles in laminated, thinly-bedded, and cross-bedded sandstones as well as in mudstones. Considered together, these features are consistent with deposition in a shallow marine setting under the influence of

waves. Fossils are preserved as casts exposed on bed interfaces in both convex epirelief and hyporelief; distal margins of the dorsal or ventral disc are often coated by a ferruginous veneer (Fig. 2).

3. Comparable stellate and discoidal fossils

The fossil described herein (PRI 42122) consists of a radiating or stellate array of inclined wedge-shaped structures, arranged around a central area devoid of ornamentation. These structures are ray-like in appearance, are unbranched, and could represent the segmented anatomy of an organism (see detailed description below). We favor a paropsonemid origin for this fossil, but given the rarity and unusual preservation of such specimens in similar Paleozoic strata, it is worthwhile to compare it to morphologically similar stellate and discoidal fossils, including: i) cnidarian medusae; ii) agnathan fish with circular mouths, such as *Pipiscus zangerli*; iii) the oral cones of anomalocaridid arthropods; and iv) discoidal to quasi-coiled radiate problematica including paropsonemids, Maoyanidiscids, *Eldonia*, and *Eldonia*-like forms such as *Discophyllum*.

Paleozoic hydro- and scypho-medusae bear radial structures, can be of similar size, and are known from coeval depositional environments. Medusae share similarities with PRI 42122, because they are rarely preserved bed-parallel, due to folding, tearing, shearing, or distortion by taphonomic processes (Young and Hagadorn, 2010). Although individual medusa fragments might share broad similarities with other discoidal fossils (Fig. 2E, F), bona fide medusae are usually characterized by specimens that display concentric structures and preserve evidence of tentacles, oral arms, and transport (see reviews in Stanley Jr., 1986; Young and Hagadorn, 2010). Because PRI 42122 does not have concentric structure nor oral arms or tentacles, nor any evidence for pliability, anterior-posterior, or aboral-adoral orientation, it is not likely to be a medusa.

The Carboniferous agnathan fish *Pipiscus zangerli* has a sphincter-like mouth characterized by ~23 tapering ray-like segments, which surround an area with little internal structure (Bardack and Richardson Jr., 1977). Like PRI 42122, pipiscid mouth segments are inclined relative to bedding (Fig. 2G). In *Pipiscus*, however, these segments are arranged in a funnel-like shape that has a more elevated exterior region separated from the interior region by a concentric notch. Pipiscid segments also bifurcate distally, just outside its medial concentric step, and have a sharp exterior margin. Considered together, these features are more akin to radial septae of corals and archaeocyathid sponges than they are to the fossil described herein, or ironically, to the mouths of

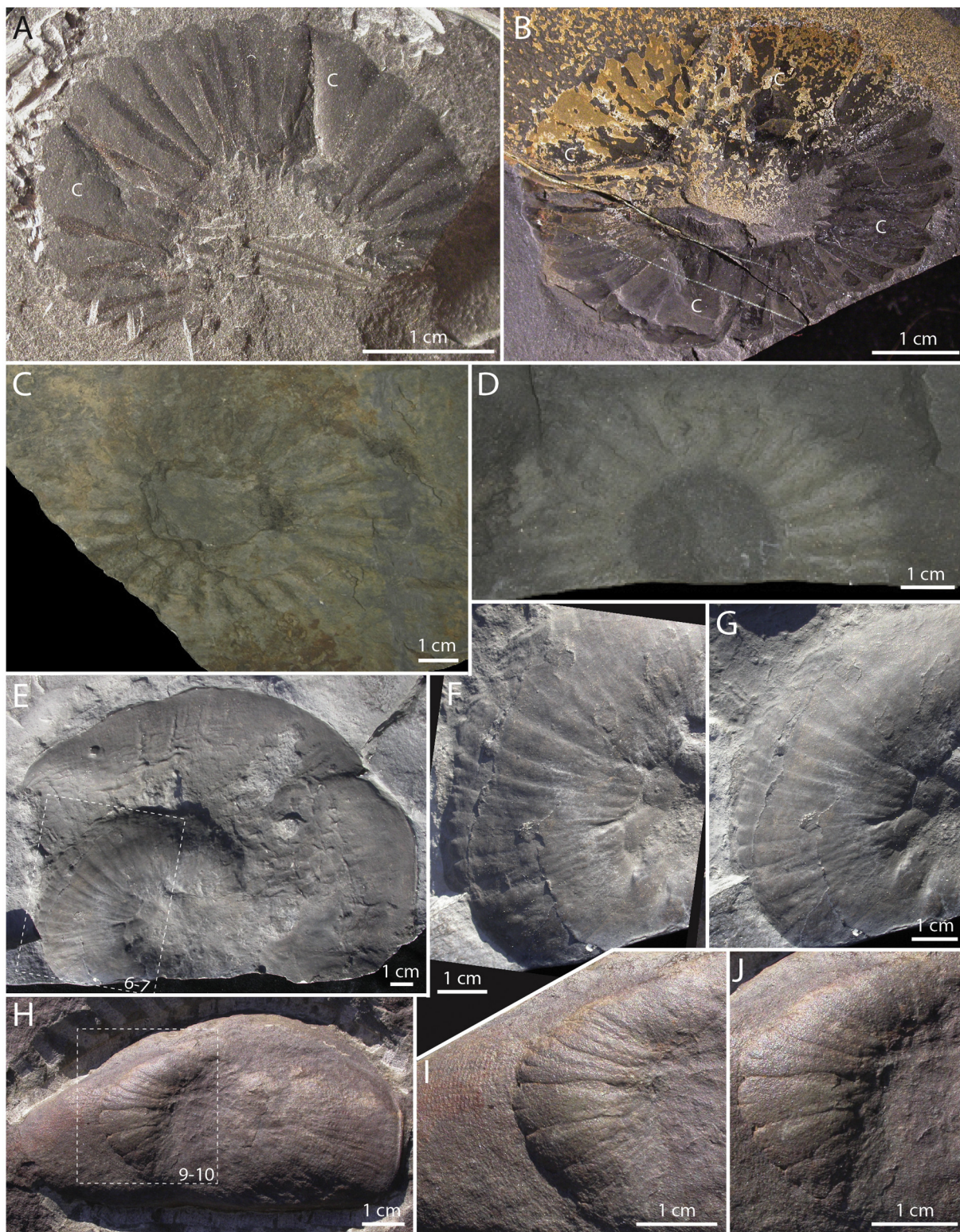


Fig. 2. Photographs of PRI 42122 and comparable discoidal fossils. (A, B) Plan and oblique-view images of PRI 42122, illuminated under low-angle light from upper left. White arrowheads in (B) demarcate the transverse ribbing that characterizes two of the inter-segment grooves. (C, D) low-angle illumination of the two sets of transverse ribbing, and the junction of the segments with the central region of the fossil. White arrowheads in (C) highlight a few of the segment-parallel striations typical of inter-segment areas, and black arrowheads illustrate a few of the segment-parallel striations visible on the flattened centers of the rays. (D) Close-up of inter-segment lineations and interior of segment tips. (E) Intra-umbrellar portion of the rhizostome medusa, *Rhizostomites admirandus* with central disk visible between partially decomposed chevron-shaped muscle fibers (Paläontologisches Museum München, 1913 I 56). (F) Fragmentary specimen where the central disk has detached from the main medusa umbrella (Paläontologisches Museum München, 1954 I 198). Like anomalocaridid mouths (Fig. 3A, B), discoid contains 32 radial divisions, but these consist of 16 paired divisions that are connected to the round margin of the central subgenital area. (G) The hypothesized mouth of *Pipiscus zangerli* (Field Museum PF 8344), illustrating the 23–46 radial divisions, consisting of an inner division that bifurcates toward the discoid's exterior.

other extant agnathan fishes (see also Butterfield, 1990).

If one reconstructs the missing portions of PRI 42122 by making a mirror image of the more complete half of the fossil, it would have 30 or 32 wedge-shaped segments. Larger segments occur at roughly 0–90–180–270° increments around the fossil and the interior of the fossil has a broadly diamond-shaped pattern. All of these features are shared with the mouths or oral cones of anomalocaridid arthropods (Fig. 3A, B; Collins, 1996), including Devonian fossils described by Köhl et al. (2009) that we interpret as *Hurdia*-like anomalocarids (see also Ortega-Hernández, 2016). However, it is difficult to identify which of

the segments on PRI 42122 might correspond to the four large cardinal plates present in all known anomalocaridid mouths (c in Fig. 3A, B), and the interior tips of the segments do not bear pointed or serrated tips as do the pointed plate tips of Cambrian anomalocaridids. Moreover, original cuticle is not present, even in the inter-segment cracks, where anomalocaridid cuticle is often preserved even in highly weathered specimens (Hagadorn, 2009). Some anomalocaridids, however, lacked or had lightly sclerotized oral cones (e.g. *Lyrarapax*, *Aegirocassis*; Van Roy et al., 2015; Cong et al., 2016) so absence of that feature is not entirely diagnostic. PRI 42122 does have a carbonaceous film atop it



(caption on next page)

(MacGabhann et al., this volume), a feature common to Cambrian anomalocaridid mouths (Hagadorn et al., 2010) and possibly reflecting relict sclerotization of their oral cone. Therefore, despite comparable sizes, superficial morphological similarity and composition, an anomalocaridid origin for this fossil is difficult to reconcile.

The problematic fossils *Actinophyllum spinosum* Straw, 1926 and *A. plicatum* Phillips, 1848, are superficially similar to PRI 42122 because

they are ovoid in plan view, are from similar age rocks, and have radial arrays of segments or rib-like structures. *Actinophyllum*, known from the Lower Devonian of England, is a particularly attractive comparison (Barrois, 1891) because its radial ‘ribs’ curve toward the bedding plane and one of the two known specimens has 30–32 segments like PRI 42122 (the other *Actinophyllum* specimen has 45 segments, but see Phillips (1848) and Straw (1926)). *Actinophyllum* differs, however, in

Fig. 3. Comparable stellate to discoidal Paleozoic fossils and known specimens of *Paropsonema cryptophya*. (A, B) Anomalocaridid mouths (i.e., “*Peytoia*”) that have been distorted transversally or obliquely relative to the horizontal plane of the mouth. Such preservation is common and makes it difficult to recognize the four cardinal plates (“c”). It also distorts the plates (i.e., segment equivalents for PRI 42122) such that they thin or thicken laterally (National Museum of Natural History NMNH 368584, American Museum of Natural History AMNH FI22492, respectively). (C, D) *Glockerichnus radiatus*, including high relief and low relief preservation, respectively. Specimen in C illustrates a quasi-rectangular ‘structureless’ central area surrounded by stellate ray-like structures; this region is comparable to those in PRI 42122 and in *P. cryptophya* specimens. (Sedgwick Museum A54997, A40374, respectively). (E–J) *Paropsonema cryptophya*, including insets which illustrate the radially arranged segments of the coiled gut. To illustrate the low-relief features of the gut, the specimens are illuminated from a variety of angles, including from the bottom (E), top (H), upper right (F, I), and upper left (G, J). The gut or sac of *Paropsonema* has significant relief, has ray-like divisions that appear to plunge into the horizontal plane of the fossil, and surrounds a ‘structureless’ central area. The orange-brown patina at left end and top of (I) highlights the ferruginous (often hematitic) nature of many *Paropsonema* specimens, perhaps representing weathering of pyrite after marcasite that coated specimens shortly after burial (sensu MacGabhann et al., this volume). (E: NYSM E103, H: NYSM 6817). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

that it has a very small or no central area (i.e., its radial ribs meet at the center), and it is much smaller than the fossil described here.

Specimens of the paropsonemid *Discophyllum peltatum*, are also superficially similar. Yet they have many more ($n = 100$) radial structures than does PRI 42122, and their structures converge in the middle of the fossil, leaving no structureless central area. Thus, although PRI 42122 may be a paropsonemid, it should not be placed in *Discophyllum*.

There are several stellate trace fossils that have features in common with PRI 42122, including forms that occur in approximately coeval strata of New York (Corbo, 1979). For example, *Volkichnium volki Pfeiffer, 1965* and many ichnospecies of *Glockerichnus* bear superficial similarity to PRI 42122 (see Orr, 1996), but they tend to have fewer ray-like segments and their rays are only quasi-radial in their arrangement (e.g., the inner tips of their rays are often shingled in a clockwise or counterclockwise direction). The lengths of their rays are highly variable, which when viewed in plan view, yields a jagged, non-ovoid and non-circular exterior trace margin – in contrast to the smooth oval margin of PRI 42122, of medusae, and of the problematica described below. In contrast, *Glockerichnus radiatus* Etheridge and *Lorenzina apenninica* Gabelli share many morphologic and preservational similarities with PRI 42122. Both stellate traces are characterized by circular to oval arrays of radiating wedge-shaped probes that surround a structureless circular region. In some examples, this circular region is oval (Fig. 3D) to diamond-shaped (Fig. 3C; also see Fig. 5a of Orr, 1996) like PRI 42122. *Lorenzina*, most widely known from Cenozoic flysch (Harrington and Moore, 1956; Crimes, 1977; Uchman, 1995), is typically preserved in convex hyporelief with a stellate pattern, but differs from PRI 42122 because: i) most figured specimens are considerably smaller; ii) most specimens bear fewer rays (typically 16–22); iii) some specimens exhibit shingling of rays; and iv) the distal portions of rays do not touch one another, but are loosely arranged like spokes. *G. radiatus*, known from the Ordovician of Ireland (Etheridge, 1876; Crimes and Crossley, 1968; Crimes et al., 1992; Orr, 1996), is as large or larger than (ca. 6–12 cm diameter), and shares many morphologic and preservational similarities with PRI 42122; in some specimens the distal tips of rays adjoin one another like the ray-like segments do in PRI 42122 (Fig. 3D). *G. radiatus* differs, however, in that it may or may not possess spoke-like arrangements of its distal rays and no known specimen of *G. radiatus* has the ~32 segments that PRI 42122 has. This numerical difference is not insignificant because comparably sized *G. radiatus* have 18–24 rays, which prohibits explaining the difference between PRI 42122 and *G. radiatus* as resulting from: i) ontogenetic differences such as a ‘juvenile’ specimen having fewer rays than an ‘adult’ specimen; or ii) greater time available to produce additional radiate burrow probes. Even *Lorenzina*, which is much smaller, has fewer rays. Thus a trace fossil origin for PRI 42122 is not supported by the morphological data.

Given this context, we follow Friend (1995) in favoring an affinity of the PRI 42122 specimen with the discoidal soft-bodied fossil, *Paropsonema cryptophya* (“*Discophyllum cryptophya*” in Friend, 1995). As shown in Fig. 3E–J, the horseshoe-shaped alimentary canal of *Paropsonema cryptophya* has a central region that is depressed relative to the bedding plane, like PRI 42122, and is divided into segments which

radiate outward from the center of the animal (see also plate 1.8 of Clarke (1900) and figs. 4vi and 4.5b of Friend (1995)). PRI 42122 differs in that its stellate segments do not bifurcate distally and it does not preserve the outer lobes, radial canals, and prominent transverse ribbing present in some *Paropsonema* specimens.

4. The paropsonemids

For this study, we examined the PRI paropsonemid as well as *Paropsonema* specimens from the NYSM, including specimens 6817, 6818, E103, E548, 445–450, and eight comparable unnumbered specimens or casts of different material.

4.1. Observations

PRI 42122 consists of a radiating or stellate array of inclined wedge-shaped unbranched segments, arranged around a central area devoid of structure. The specimen has an oval external outline and is 7.4 cm long; mirror-imaging of the better preserved half of specimen suggests that the original specimen was ≤ 5.8 cm wide. There are 22 segments present, with complete segments 1.7 to 2.3 cm long and 1.5 to 9.0 mm wide, and up to 3.1 mm of vertical relief exists from the interior to exterior of each segment. Segments vary considerably in size; each is symmetrical, and broadens distally. The broad ends are rounded to quasirectangular and curve upward. Segments at the narrowest and widest ends of the fossil are larger than those in between. Several (≥ 4) segment tips are ferruginous (Fig. 2D). Segments on the broken specimen are arranged circumferentially for $\sim 280^\circ$. The structureless central region is shaped like a rectangle whose sides are convex inward, with the narrowest portion 0.8 cm wide and the longest portion 3.1 cm long. The entire fossil is inclined relative to bedding by 12° (ca. 5 mm) and the basal surface of individual stellate segments is inclined inward relative to the plane of the fossil as much as 9° . Some grooves between segments bear segment-parallel striations. Two inter-segment depressions on PRI 42122 bear eight to eleven 1–3 mm wide ridges; these ridges are parallel to one another and perpendicular to the long axes of segments.

4.2. Interpretation

PRI 42122 is directly comparable to arcuate to coiled structures found in the center of two dorsally preserved specimens of *P. cryptophya* (NYSM 6817, E103). NYSM 6817 is a small (9.1×4.8 cm wide) specimen that appears to be curled in half like a folded fried taco tortilla; it bears an arcuate structure on one end of its long axis that appears to be divided into a series of adjoining ~ 16 ray-like segments. The arcuate structure is $\sim 2.7 \times 3.4$ cm wide, may have up to 3.5 mm of vertical relief, is inclined by $\sim 21^\circ$ relative to the horizontal plane of the fossil and has divisions or segments which are 0.8 to 1.8 cm long and taper inward toward a structureless interior region. The segment tips are lobate and some distal segment tips are split; some segment tips bear weak transverse striations. Transverse striations do not occur along the midline of inter-segment divisions. Distal tips of these segments are

inclined from 10 to 70° with respect to the plane of the disc lobe, and appear to plunge into the disc. Following Friend (1995), Zhu et al. (2002), and MacGabhann (2012), PRI 42122 is interpreted as the coiled segmented alimentary canal or sac of a paropsonemid, a group that likely represents stem deuterostomes. We tentatively assign it to *Paropsonema cryptophya* (Clarke, 1900), a taxon that has a challenging taxonomic hierarchy (MacGabhann, 2012), because it falls within *Incertae sedis*.

5. Other dorsally preserved paropsonemids

NYSM E103 is considerably larger (~21 cm by > 12.5 cm wide) than PRI 42122, is mostly preserved in a near bed parallel position, and contains an arcuate to coiled structure in its center that appears to be divided into a series of ray-like segments. The morphology of these segments is identical to that of NYSM 6817, but the segments surround a large structureless central region ~ 3 × 2 cm wide that illustrates the imperfect radial (i.e., offset shingle) arrangement of the segments in the coiled structure. In this central region the inner ends of the segments are jagged. The arcuate to coiled structure is inclined to the horizontal plane of the fossil by ~15°, and is notable because it bears up to 28 segment-like divisions, with approximately 25 of these spread across 180°. Four other specimens (NYSM 450, 445, 6818, E548) not illustrated here preserve the weak outline of some of these segmented structures, in one case also these are arranged in an arcuate array. Thus, following Friend (1995), Zhu et al. (2002), and MacGabhann (2012) we interpret these paropsonemid segmented structures as the coiled alimentary canal or sac of the animal. In paropsonemid specimens where this segmented structure is preserved in three-dimensions and sediment-filled, it is mantled by the external integument of the animal, sometimes with only weak traces of external disc ornamentation visible (e.g., Figs. 3F, I).

The discoidal fossils *Discophyllum peltatum* Hall, 1847, *Eldonia eumorphia* Sun and Hou, 1987, *Eldonia ludwigi* Walcott, 1911, *Maoyanidiscus grandis* Sun and Hou, 1987, *Paropsonema cryptophya* Clarke, 1900, *Paropsonema mirabile* Chapman, 1926, and *Pararotadiscus guizhouensis* Zhao and Zhu, 1994 share sufficient synapomorphies that they merit formal grouping but can be informally referred to as eldonids until publication of MacGabhann and Murray (accepted). All of these fossils have coiled sacs or alimentary canals which are often segmented and which occur in the center of the discoidal body (Sun and Hou, 1987; Chen and Zhou, 1997; Zhu et al., 2002; MacGabhann, 2012). Although such structures are typically flattened, they are rarely three-dimensionally preserved in convex relief on dorsally preserved specimens. In such situations, the alimentary canal or sac is sometimes segmented into a stellate to radiating array of tapering wedge-shaped ‘rays’ that plunge into the outer lobe of the disc (e.g., fig. 4B of Chen et al., 1995; MacGabhann, 2012).

6. Challenges and implications

Perhaps the most pressing question regarding *Paropsonema* is ‘what type of animal is it?’ Our observations on the three-dimensionally preserved arcuate segmented alimentary structure in *P. cryptophya* align with it being a homologous structure shared by the paropsonemids and the eldonids. Recent insights from exceptionally preserved tentaculate fossils from the Burgess Shale and Chengjiang (Caron et al., 2010), are internally consistent with the hypothesis that paropsonemids are stem-group deuterostomes allied with early hemichordates or echinoderms (Friend, 1995).

Paropsonemids, including the three dorsally preserved specimens illustrated here, are usually preserved in two dimensions as flattened, twisted or distorted discs, but some preserve three-dimensional sand-filled tissues such as the segmented alimentary tracts illustrated here. The rare dorsal preservation of stellate to segmented structures in the center of all these fossils may result from a common taphonomic or

possibly a dietary strategy for such animals. If the alimentary canal is filled with sediment as a result of transport or burial of the animal, then one needs to explain how fluids transported sediment into the mouth and gut, without damaging the rest of the lobate-discoidal integument of the animal. Given the subtidal environments of deposition of paropsonemids and eldonids, one cannot invoke the active or passive sediment stuffing processes that occur with soft-bodied sac-shaped animals that are stranded in intertidal-supratidal environments (see Hagadorn et al., 2002 or Young and Hagadorn, 2010 for reviews). Moreover, these groups are never preserved within the sediment (except when transported in event beds) nor are they associated with burrows. It seems more likely that these animals had an epibenthic mode of life, perhaps ingesting sediment while living atop or just above the seafloor (Friend, 1995; Dzik et al., 1997; Van Roy, 2006; Caron et al., 2010).

Some of these questions could be answered by sectioning the specimens, but we have not done so because so few specimens of *Paropsonema* are known, and only one specimen is known from the Freeville locality. Yet without sectioning of specimens with three-dimensional preservation of the alimentary canal, and without collecting new material, it is not possible to determine how or why this portion of these animals is preserved in convex relief and filled with sediment, when many other parts of paropsonemids and eldonids are preserved in two dimensions, as flattened, folded, or distorted impressions—but see MacGabhann et al. (this volume) for a potential taphonomic framework to explain the observed differential preservation. Additionally, it is unclear why some specimens bear transverse striations atop the segments of what appears to be the alimentary canal, whereas others do not. MacGabhann and Murray (accepted) suggest that these striations could represent radial fibers – structures that suspended the coiled sac within a coelomic cavity.

7. Conclusions

It is important to illustrate fossils like *Paropsonema* because they provide a ‘search image’ for discovering rare fossils that help resolve our understanding of early animal evolution and ecology. Indeed, the paropsonemid from Freeville (PRI 42122), found by an avocational paleontologist nearly a century after the last paropsonemid was collected in New York, illustrates the contributions that can be made in ‘well-studied’ rocks by individuals with keen eyes and a willingness to look. If correctly interpreted, this specimen extends the geographic range of paropsonemids to another region in New York, extends their stratigraphic range, and illustrates an additional mode of soft-tissue preservation on dorsal surfaces of discoidal fossils.

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