

1 **A LATE ORDOVICIAN PLANKTIC ASSEMBLAGE WITH EXCEPTIONALLY**
2 **PRESERVED SOFT-BODIED PROBLEMATICA FROM THE MARTINSBURG**
3 **FORMATION, PENNSYLVANIA**

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14 *RRH: LATE ORD. PLANKTIC ASSM. WITH EXC. PRES. FROM PA*

15 *LRH: MEYER ET AL.*

16 Keywords: Burgess shale-type preservation, Problematika, GOBE, Ordovician plankton,
17 Martinsburg Fm.

18 **ABSTRACT:**

19 **Here we report a locality containing exceptionally preserved (soft-bodied)**
20 **fossils of mid-Late Ordovician age from the geologically complex Martinsburg**
21 **Formation in central Pennsylvania. The fossils, which resemble specimens from**
22 **Burgess Shale-type deposits, include enigmatic specimens (problematika) and**
23 **phyllocarid arthropods (with preserved appendages) which are associated with**

24 **graptolites. The locality is notable for preservation of a low diversity community of**
25 **soft-bodied planktic animals, likely captured and rapidly buried by a turbidity**
26 **current. The problematica lack sufficient anatomical detail for confident systematic**
27 **placement; however, they can be superficially compared to a number of possible**
28 **metazoans including: nominally/non- shelled molluscs (including veligers),**
29 **cnidarians, lophophorates, or possibly aberrant tube-dwelling priapulids or**
30 **polychaetes. Overall, the problematica may belong to one (or several) extinct clades**
31 **or some unknown clade of animal life. The complex geologic history of the region**
32 **has reduced the resolution of the problematica’s original exceptional preservation,**
33 **yet the fossils retain many key features. Hence, this locality has implications for our**
34 **understanding of exceptional preservation, its alteration over geological history, and**
35 **the planktic communities of “The Great Ordovician Biodiversification Event”**
36 **(GOBE) in the planktic realm.**

37 **INTRODUCTION**

38 The Great Ordovician Biodiversification Event” (GOBE) is a time of rising biodiversity
39 which resulted in an increase in the ecological prominence of benthos suspension feeders
40 and the proliferation of the planktic realm (Webby, 2004; Harper et al., 2015; Algeo et
41 al., 2016; Servais et al., 2016). Causes of the GOBE are mainly credited to an Early to
42 Middle Ordovician greenhouse climate that promoted a rise in sea level and the
43 development of ecospace partitioning in the form of planktic predators, including
44 graptolites and radiolarians, followed by a terminal Late Ordovician glaciation
45 (Bambach, 1983; Servais et al., 2010) and sea level fall.

46 The increased presence of available food, such as plankton, in the water column
47 has been suggested as a driver for this radiation (Servais et al., 2009; Servais et al., 2016).
48 Proposed agents also include increased orogenic activity (Miller and Mao, 1995), the
49 appearance of new substrates (Rozhnov, 2001), the large-scale diversification of
50 phytoplankton (Servais et al., 2010), asteroid impacts (Schmitz et al., 2008), and cooling
51 of the oceans (Trotter et al., 2008). The GOBE is a multifaceted event with very
52 pronounced taxonomic, geographic and temporal dimensions, making it difficult to
53 determine what trigger(s) set in motion this complex event in the early Paleozoic.
54 Additionally, our understanding of the GOBE chiefly derives from the shelly fossil
55 record (Servais et al., 2010; Servais et al., 2016) because few exceptionally preserved
56 fossil assemblages (Konservat-Lagerstätten) had been reported from the Ordovician
57 until recently (Schiffbauer and Laflamme, 2012; Van Roy et al., 2015; Muscente et al.,
58 2017). With the exception of the Fezouata Biota most of these faunas generally represent
59 marginal or otherwise unusual environments and atypical, low-diversity communities.
60 Most have limited usefulness in understanding evolution of the planktic realm during the
61 GOBE.

62 Exceptionally preserved fossils, those that preserve non- or weakly
63 biomineralized organisms (Allison and Briggs, 1993; Schiffbauer et al., 2014), provide
64 key insights into ancient biodiversity (Muscente et al., 2017); especially they include
65 species with low preservation potentials that drive up measures of taxonomic and
66 ecological richness and extend the ranges of known species (Farrell et al., 2009; Van Roy
67 et al., 2010; Briggs, 2014). Notable examples of exceptionally preserved fossil localities
68 in the Ordovician include: the Fezouata and Tafilalt Biota of Morocco (Van Roy et al.,

69 2010; Van Roy et al., 2015), Beecher's Trilobite Bed and similar sites in New York State
70 (Farrell et al., 2009), the Soom Shale of South Africa (Gabbott et al., 2017), and the
71 Llanfallteg and Afon Gam biotas of Wales, UK (Botting et al., 2015; Hearing et al.,
72 2016). Many of these fossils occur as 'Burgess Shale-type' (BST) assemblages
73 (Butterfield and Nicholas, 1996; Meyer et al., 2012; Schiffbauer and Laflamme, 2012) of
74 soft-bodied (non-biomineralized) organisms, however other preservational modes (Cai et
75 al., 2012) are also present such as pyritization (Beecher's) and Ediacaran-type (Tafilalt).
76 Conditions leading to BST preservation were more common in marine environments in
77 the Ediacaran and especially the early-middle Cambrian, with the possibility of the late
78 Cambrian; see Lerosey-Aubril et al. (2017), but is restricted post-Cambrian (Meyer et al.,
79 2012; Schiffbauer and Laflamme, 2012; Muscente et al., 2017).

80 This paper describes a new locality from a geologically complex area in central
81 Pennsylvania, where mid-Late Ordovician marine clastic rocks of the Martinsburg
82 Formation contain exceptionally preserved fossils. These fossils include enigmatic
83 spindle- or conotubular-shaped animals (problematica) and phyllocarid arthropods, found
84 with graptolites. The problematica are compared to nominally/non-shelled molluscs,
85 cnidarians, lophophorates, or possibly aberrant tube-dwelling priapulids or polychaetes;
86 though they may belong to an extinct clade.

87 **GEOLOGIC SETTING**

88 The faunal suite of graptolites, problematica, and phyllocarids (fragments and a
89 single whole specimen) are from the Martinsburg Formation near Hummelstown, east of
90 Harrisburg, PA, USA (40.296443 N, -76.726004 W). The regional geology (Fig.1) is
91 structurally complicated (Ganis and Wise, 2008; Wise and Ganis, 2009) and the rocks are

92 generally anchizone rank, defined by illite crystallinity and Conodont Alteration Indexes
93 (CAI). Conodonts from the Martinsburg Formation in the general vicinity have a CAI of
94 4.5, indicating a thermal exposure between approximately 275-300 degrees centigrade,
95 which agrees with the illite crystallinity data (John Repetski, USGS, personal
96 communication). Physiographically, the site lies within the Great Valley Section of the
97 Piedmont Province in the Appalachians. The Martinsburg Formation has been
98 tectonically affected by Taconic (Late Ordovician) and Alleghenian (Middle to Late
99 Paleozoic) orogenies, which left the rocks highly sheared, folded and faulted (Wise and
100 Ganis, 2009). Large scale overthrusting regionally positioned the low greenschist
101 Cocalico terrane over the Martinsburg in this area of the Great Valley (Wise and Ganis,
102 2009).

103 The road-cut section (see figure 1B) is primarily grey-black shale with penetrative
104 multi-oriented cleavage, but the fossil-bearing strata (~10 cm in thickness) are more
105 thickly bedded siltstones, with nominal bedding-parallel cleavage (macro-scale
106 observation). Graptolites collected from the siltstones show little damage from cleavage
107 generation. However, the orientations of some specimens of problematica show evidence
108 of partial damage by incipient cleavage acute to the bedding, which is not otherwise
109 apparent in slab samples. Collecting at this site has been light, and additional excavation
110 is warranted.

111 Graptolites of the *Diplograptus foliaceus* Zone (+/- *Climacograptus bicornis*
112 Zone, see Figure 2B) were recovered indicating a position in the lower Martinsburg
113 Formation, Late Ordovician, Sandbian age. The interpreted depositional environment
114 here, and for the Martinsburg Formation in general, is a turbidity-driven flysch, infilling

115 the Taconic foreland basin (McBride, 1962; Ganis et al., 2001; Ganis and Wise, 2008).
116 The Martinsburg foreland fill consists almost exclusively of clastic strata of deep-water
117 origin. Graptolites are common in black shales deposited under dysoxic to anoxic bottom
118 water conditions, and are generally absent in grey-green oxic facies. Graptolites
119 accumulated in the sediment via deadfall or were captured within the water column from
120 sedimentological events originating from activated turbidity currents (where they can be
121 found in coarser sediment). Overall, the Hummelstown site is a thick (at least tens of
122 meters thick) section of mostly shale and lesser siltstones, compatible with typical
123 Martinsburg flysch.

124 **METHODS**

125 All figured specimens are repositied in the collections of the National Museum of
126 Natural History (Smithsonian Institution). Reflected light photographs were made with a
127 Canon PowerShot SX20 IS, Panasonic (Lumix) DMC-FZ300, and an Olympus DP-25
128 attached to a binocular microscope. Digital photographs were processed in Adobe
129 Photoshop CS5, and composite images (Figs. 2–5) were stitched together using the
130 ‘Photomerge’ option in Adobe Photoshop CS5.

131 Electron microscopic analyses (Figs 2–3) were conducted using an FEI Nova
132 NanoSEM 600 field emission environmental scanning electron microscope (ESEM) in
133 high vacuum mode using secondary (topographic) and backscattered (atomic number
134 contrast) electron detectors. Energy-dispersive X-ray spectroscopic (EDS) point spectra
135 and elemental maps (of fossils on unpolished bedding surfaces) were generated using an
136 integrated ThermoFisher energy-dispersive X-ray detector and a Gatan
137 cathodoluminescence detection system. Identical operating conditions were maintained

161 specimens. The graptolites are preserved as collapsed tubaria with some residual relief.
162 They generally possess fair to good anatomical definition typical of carbonaceous
163 compressions of graptolites with completely sclerotized (hardened) tissue. In addition to
164 fragments, we collected a single complete specimen of a phyllocarid arthropod (Fig. 2C).
165 Although its appendages are not well preserved and the systematics of the specimen have
166 not been evaluated, it possesses a distinctive cuticular carapace, abdomen with 5-7
167 segments, and pointed telson.

168 A typical HTP fossil has two main morphological features; a cone-shaped
169 posterior body and an anterior external body mass which appears to protrude beyond the
170 aperture-like structure (Fig. 4A; considered a model example). The boundary between the
171 cone-shaped body and the external mass is seen as a discontinuity across the cone's axis
172 (Fig. 4A, 5), except where the exterior body is absent (or possibly has been retracted
173 within the cone-shaped posterior body). Most of the fossils are smooth-sided and straight,
174 but some show a slight curvature (Fig. 2A, D, and 4B). Overall, they are approximately
175 3–10 mm long and 1–3 mm wide at the aperture-like structure. The external body mass
176 ranges in size from relatively small (<1 mm) to a length similar to the posterior cone-
177 shaped body (Fig. 4A). There are two very general morphological groups of cone fauna,
178 one, which is long and narrow, and the other, which is shorter and wider (Figs. 4B, 5).
179 Often, the narrowing apex terminates in a spindle-like shape as a rod (Fig. 4A).

180 We found no evidence of branching, holdfasts, or connection points at the apex of
181 any specimen (Fig. 3B, 4A). Likewise, we found no discernable internal anatomical
182 features within cone-shaped posterior bodies, and the external mass consistently exhibits
183 an amorphous appearance save for the small spikes or flaps seen on some specimens.

184 Although, this condition may simply reflect marginal preservation, it may be considered
185 that this is the outline expression of an anatomically simple, pliable body (proposed
186 taxonomic affinity is discussed below). None of the cone-shaped posterior bodies possess
187 any unambiguous evidence of biomineralization (Fig. 3B), but we cannot rule out the
188 possibility that the fossil represents an originally biomineralized skeletal element, which
189 underwent taphonomic demineralization during diagenesis or weathering (Muscente and
190 Xiao, 2015). Currently, there is no evidence for moldic impressions of the HTP fossils.

191 The HTP fossils are preserved as carbonaceous compressions, which can be seen
192 in the dark-black appearance (low atomic mass, or Z) in backscattered electron (BSE)
193 imagery, the large carbon signal from EDS point analysis, and their black color in hand
194 sample (Figs. 2F, 3A–C). Under magnification in reflected light microscopy, the fossil
195 specimens have a golden-colored sheen in reflected light due to the abundance of pyrite
196 framboids (now Fe-oxide pseudomorphs with no Sulphur present, see Figure 2E) and
197 many fossils are surrounded by pyritic envelopes (Figs. 3). Elemental EDS analysis also
198 show that some of the HTP fossils also contain relatively higher concentrations of Si than
199 their surrounding matrixes (Fig. 2F). The Si likely occurs within thin Fe-rich clay veneers
200 on the fossils, which we observed in BSE images (Fig. 3B). We did not detect the Si
201 signal of these veneers in all specimens (Fig. 3B–C), but this may represent a
202 consequence of their thinness and the low surface-sensitivity of EDS analysis (Orr et al.,
203 2009; Muscente and Xiao, 2015). Tectonic cleavage can contain high Si levels, and
204 although it cuts through the HTP fossils, it is not expressed in the graptolites or
205 phyllocarids in a similar manner). While this cleavage breaks up the fossils and degrades
206 the resolution of minute features, overall, fossil morphology remains intact.

207 **DISCUSSION**

208 *Paleoecological Considerations*

209 The graptolites, phyllocarids, and HTP specimens occur in dense mixed
210 assemblages at the Hummelstown locality. The close association of these fossils suggests
211 the HTP represent organisms with planktic habits and possible ecological relationships
212 with the other fauna. However, due to the enigmatic taxonomic affinities of the HTP,
213 their ecology is unknown. Among the mixed specimens of graptolites and problematica,
214 one pair of specimens (Fig. 3D–E) appears to show physical attachment between
215 organisms of the two groups, but this example may represent an accident of fossil
216 placement. Additional specimens of this type would be required to indicate ecological
217 interaction.

218 No unusual sedimentological conditions are apparent at the Hummelstown site
219 that might explain the special conditions necessary for preservation of soft-bodied
220 organisms, although that topic deserves further study. However, the role of the post-
221 burial alteration (either geochemically or physically), also needs to be better understood
222 (see below).

223 *Evidence for Burgess Shale-Type Preservation*

224 The HTP specimens collected from the Hummelstown locality resemble BST
225 fossils in terms of their overall preservation. In general, BST fossils represent non-
226 biomineralized tissues (Butterfield, 2003) often preserved via pyritization or clay
227 minerals (Schiffbauer et al., 2014). Fossils of phyllocarid carapaces often signify non-
228 biomineralized elements (Caron and Jackson, 2008; Gabbott et al., 2008) and there is
229 evidence the HTP fossils may represent labile tissue (Fig. 4, 5). The EDS spectra of the

230 HTP contain prominent carbon signals, consistent with the preservation of organic
231 matter, but we cannot rule out that the HTP fossils (with the possible exception of the
232 external body mass) were originally biomineralized skeletal elements, which were
233 taphonomically demineralized during diagenesis and/or weathering, leaving behind
234 carbonaceous residuals of the shells' organic matrices (Muscente and Xiao, 2015).

235 The occurrence of the fossils in a black shale suggests preservation occurred in a
236 deep water, organic-rich, anoxic setting, which is very favorable to conservation of
237 organic matter and formation of diagenetic pyrite. A absence of bioturbation suggests that
238 the fossils experienced rapid burial in a benthic environment that contained effectively no
239 benthic mobile animals (or at least at the level at which the fossils were buried). Pyrite
240 framboids found with the HTP fossils are similar to those found in association with
241 *Wiwaxia* sclerites of the Burgess Shale (Butterfield, 2003; Butterfield and Harvey, 2012)
242 and trilobites of Beecher's Trilobite Bed (Farrell et al., 2009); in addition to fossils at
243 various other localities (Cai et al., 2012; Schiffbauer et al., 2014; Muscente et al., 2017).
244 Higher concentrations of Fe-oxides around the Hummelstown fossils provide further
245 evidence for microbial cycling of sulfur (Fig. 3C). In reflected light (Fig. 2A), the HTP
246 differ from the associated graptolites (which have less of a sheen), perhaps due to
247 different body integument types and the volatility of those tissues (Gabbott et al., 2004).
248 Elemental analysis of the HTP specimens supports a much lighter (or absent) taphonomic
249 mineralization. Whereas some of the sclerotized graptolites are heavily pyritized), the
250 HTP are primarily non-mineralized carbonaceous material. Since pyritization results from
251 the degradation of organic matter and the precipitation of sulfide by sulfur-reducing

252 bacteria, the differing amounts in the two fossils suggests that the problematica had much
253 less organic matter in their bodies than the graptolites.

254 The relationship between clay minerals and exceptional preservation are still
255 under study (Meyer et al., 2012; Schiffbauer et al., 2014). Various studies of authigenic
256 (Harvey and Butterfield, 2017) and detrital clay materials (Orr et al., 1998; Orr et al.,
257 2002; Liu et al., 2016) in fossils have argued that they play a role in soft tissue
258 conservation by inhibiting autolytic decay (Meyer et al., 2012; McMahon et al., 2016)
259 Nonetheless, evidence indicates the metamorphism also plays a role in creating and/or
260 altering clays within fossils (Butterfield, 2003; Orr et al., 2003; Butterfield et al., 2007;
261 Muscente and Xiao, 2015). The origin of the clays in the HTP fossils are undetermined,
262 thus, their role in preservation is speculative. Although the overall morphology of the
263 HTP fossils is intact, the paucity of finely preserved features or internal details might be a
264 consequence of the illite crystallinity associated with the anchizone rank of the rock.
265 However, the fossiliferous rocks of the Burgess Shale are greenschist rank; see Powell
266 (2003), so anchizone rank does not preclude the preservation of fine features. Post-
267 formational metamorphic effects on exceptionally preserved fossil have received little
268 discussion in the literature, as most authors focus on the formational processes. Hence,
269 the taphonomic history of the Hummelstown locality provides a potential resource for
270 studying the effects of matrix alteration/degradation on the processes of exceptional
271 preservation.

272 *Taxonomic affinity*

273 While assigning a taxonomic affinity of the problematica is challenging, the
274 fossil's deep marine depositional environment (anoxic black shale), association with

275 pelagic graptolites (Sheets et al., 2016), soft-bodied taphonomy, and the absence of co-
276 occurring benthic faunal, infers a planktic habitat. Ordovician rocks contain few examples
277 of non-biomineralized pelagic organisms, particularly those of small size, because they
278 have an low preservational potential and high susceptibility to taphonomic degradation.
279 Hence, there are a limited number of representative small, pelagic, cone-shaped
280 organisms from the fossil record of this interval. Most cone-shaped fossils are larger than
281 the HTP, even during their early ontogenetic stages, such as with nautiloids, although
282 their early record is still under investigation (Kröger and Mapes, 2007; Kröger et al.,
283 2009; Kröger et al., 2011; De Baets et al., 2012; Landing and Kröger, 2012).

284 The tentaculitoids are unlikely to be possible candidate organisms (Wood et al.,
285 2004; Farsan, 2005; Filipiak and Jarzynka, 2009; Wittmer and Miller, 2011). The long
286 and narrow HTP superficially resemble tentaculitoids, but the latter are more heavily
287 mineralized and have a lower degree of aperatural expansion (Farsan, 2005) than the
288 HTP. Tentaculitoids have a bulbous initial chamber and many have longitudinal and
289 transverse ornamentation (which are still recognizable in decalcified specimens, see
290 Filipiak and Jarzynka (2009)). Major forms of planktic tentaculitoids like dacryoconarids
291 first appeared in the Devonian (Berkyová et al., 2009; Wittmer and Miller, 2011). Similar
292 bulbs can also be seen in externally shelled cephalopods preserved as “ghosts” or films
293 (De Baets et al., 2013).

294 Conulariids are excluded due to their much larger size and heavily biomineralized
295 external structure (Babcock, 1991; Ford et al., 2016). We found no evidence of holdfasts
296 in any of the ~50 specimens examined, so while their absence may be taphonomic, this is
297 unlikely and supports the interpretation that the HTP inhabited pelagic environments,

298 unlike conulariids. *Sphenothallus* has been variously described to have similar affinity to
299 annelids (Mason and Yochelson, 1985) or cnidarians (van Iten et al., 1992; Muscente and
300 Xiao, 2015; Vinn and Kirsimae, 2015). Regardless, *Sphenothallus* represents a
301 phosphatic or organophosphatic tubular or conotubular shell presenting as two periferal
302 longitudinal thickenings (when flattened) separated by relatively thinner walls; the shell
303 attached to the seafloor via a conical holdfast, which is not always preserved. Although
304 *Sphenothallus* is often found preserved as carbonaceous fossils, the absence of the other
305 features precludes placement of the HTP with that taxon (possible cnidarians affinities
306 other than *Sphenothallus* are discussed below).

307 Hyolithids, commonly grouped with the lophophorates (Moysiuk et al., 2017),
308 have a similar short and wide morphology as have the HTP and are often found in great
309 numbers on a bedding plane while occasionally being preserved as organic fossils
310 (Babcock and Robison, 1988; Martí Mus, 2014; Kimmig and Pratt, 2015; Martí Mus,
311 2016). However, hyolithid affinities can be excluded due to numerous factors, including:
312 surface structures, ornamentation, and general morphology (Martí Mus and Bergström,
313 2005). Although the absence of these features may reflect the poor preservation of the
314 HTP, such features are present even in hyolithids preserved as carbonaceous compression
315 (Martí Mus, 2014; Martí Mus, 2016; Moysiuk et al., 2017). Hyolithid shells rarely show
316 bending or curvature and are often (but not always) found with their biomineralized parts
317 (the helens and operculum) nearby: features which we did not observe at the
318 Hummelstown locality.

319 Certain corynoidid graptolites are degenerative forms consisting of a single large
320 sicula and one or two smaller thecae in parallel growth. Yet, they clearly exhibit

321 characteristics common to graptoloid sicular growth (fusellar rings and cortical bandage)
322 with prosicular and metasicular stages, as well as the presence of a prominent virgella
323 and nema (Maletz and Zhang, 2016). Although the large corynoidid sicula is cone
324 shaped, as is the HTP cone, the latter lacks all other characteristics associated with
325 graptolite morphology; other graptolites from this location do have well preserved
326 morphology.

327 Cone-shaped algae, which superficially resemble the HTP specimens, are often
328 preserved as organic compressions, such as *Winnipegia cuneata* (Fry, 1983).
329 Nonetheless, these algae have clear holdfasts at their apex and differ in size from the HTP
330 specimens. Some Ediacaran algae or organic forms (i.e. *Vendotaenia*) are preserved in a
331 similar manner (Meyer et al., 2016) while other early algae display branching that could
332 be broken up into smaller cone-shaped fragments (Du et al., 2017; Nowak et al., 2017).
333 However it is unlikely that the HTP fossils represent broken stipes. The regular
334 morphology of the HTP fossils, which fall within a relatively narrow size range, does not
335 exemplify any Paleozoic algae (LoDuca et al., 2017). Thus, we also exclude algal
336 affinities.

337 The known cone-shaped fossil organisms that occurred in comparable habitats to
338 the HTP fossils, which can be excluded for various reasons, were discussed above. A
339 further list of animals with the potential for affinity are discussed below, which includes
340 nominally/non- shelled molluscs (including veligers), cnidarians, lophophorates, and
341 aberrant tube-dwelling priapulid or polychaete worms. It should be noted that the cone
342 section of the problematica could be either tubicolous or visceral, but it is putatively non-
343 biomineralized. It is tempting, and perhaps prudent, to consider all the HTP fossils as

344 belonging to a single animal category. However, there is at least a possibility that the
345 population represents a mixed community of different taxa that all share the same gross
346 outward morphology and, at a minimum, two different morphotypes are present (see Fig.
347 5) based on length vs width ratios.

348 *Cnidarians*

349 The cnidarian fossil that most closely resembles the HTP is the enigmatic
350 *Cambrorhytium* from the middle Cambrian Marjum Formation, which has been classified
351 as a tubicolous cnidarian (Conway Morris and Robison, 1988). The exceptionally
352 preserved biotas from the middle Cambrian of Utah all represent BST preservation
353 deposits (Conway Morris and Robison, 1988). The overall simple cone-shape of
354 *Cambrorhytium* is similar to the HTP fossils, including a slight bend near the apex, and
355 two 'species' based on length vs width ratios (*C. major* is long and narrow while
356 *C. fragilis* is short and wide).

357 There may be evidence for an external body mass in *Cambrorhytium* (see fig. 12,
358 3b in Conway Morris and Robison, 1988). By analogy, the HTP cone would be a
359 tubicolous structure and the external mass in the HTP would be the body (with mangled
360 and matted tentacles?). Despite these similarities, the *Cambrorhytium* are much larger
361 than any of the collected HTP specimens and the presence of prominent annulations in
362 *Cambrorhytium* may exclude it as a comparable organisms (*sensu stricto*). Overall, the
363 broad range of morphological variety and life modes within Cnidaria (and those fossils
364 sometimes grouped with cnidarian affinity) might possibly accommodate the HTP fossils.

365 *Mollusca*

366 A molluscan affinity may be a viable solution, as the problematic fossils superficially
367 resemble two extant molluscan forms: pelagic thecosomatous pteropods and gastropod
368 planktotrophic veligers (possibly as a retention of juvenile characteristics by an adult
369 form, also known paedomorphy). Both of these taxa have two-part body plans, and in
370 some cases a retractable foot (possibly analogous to the external body mass of the HTP).
371 Some of the earliest gastropod fossils display apical larval shells, indicating that early
372 gastropods employed planktic larvae as early as the Late Cambrian (Bandel, 1997;
373 Peterson, 2005; Frýda, 2012; Nielsen, 2013), and the development of planktotrophy and
374 the expansion into pelagic niches by gastropods in the Ordovician
375 (Nützel et al., 2006; Nützel et al., 2007; Nützel et al., 2007). Specifically, Peterson (2005)
376 determined that gastropod veligers (planktotrophic or feeding larvae) most likely
377 appeared in the Early to Middle Ordovician.

378 During this time the appearance of actively feeding larvae coincided with the
379 emergence of multi- tiered suspension feeders and a restructuring of the planktic
380 ecosystem (Peterson, 2005; Servais et al., 2009; Servais et al., 2010). Therefore, it could
381 have been more beneficial for veligers to become holoplanktic, like extant pteropods, and
382 remain in the planktic ecosystem for their entire life cycle (Nützel and Frýda, 2003;
383 Nützel et al., 2006; Nützel et al., 2007; Servais et al., 2009; Nielsen, 2013). The HTP can
384 be morphologically compared to lightly biomineralized (now dissolved), nominally to
385 non-shelled veligers, or adult molluscs with a pteropod-like life style (based on
386 superficial morphology); thus, that type of organism is a candidate for the HTP identity.
387 However, true pteropods are only documented from the latest Mesozoic (Cuvier, 1817;
388 Janssen and Peijnenburg, 2014; Janssen and Goedert, 2016) which eliminates affinity to

389 extant or fossil pteropods. Therefore, an adult molluscan form with a similar form and
390 life-style would imply homoplasy within the Late Ordovician molluscan clade.

391 *Other Lophophorates*

392 Of the major groups of Lophophorates, Brachiopoda, and Bryozoa, can be dismissed as
393 not comparable to the HTP fossils, leaving Hyolitha and Phoronida for discussion.

394 Hyolitha is discussed above as a non-viable candidate. The Phoronida are worm-like
395 sessile dwellers, which build chitinous tubes, thus having a simple body plan like the
396 HTP fossils. The actinotroch larvae of the group are free-swimming. The fossil record of
397 Phoronida is sparse due to their lack of mineralized hard parts and limited preservational
398 potential. May (1993) identified the presence of phoronids based on phoronid-like
399 borings, *Talpina* from the Devonian, but provided no evidence of soft-bodied fossils
400 themselves. Without better exclusionary criteria revealed by taxonomic detail, the
401 potential accommodation of the HTP fossils within the Phoronida, as an aberrant pelagic
402 form, can be held open wherein the external mass is interpreted as a lophophoric process.

403 *Aberrant tube-dwelling priapulids or polychaetes*

404 The lack of annulation or segmentation in the HTP fossils is not necessarily indicative of
405 a preferred placement into either priapulids or polychaetes (Liu et al., 2014; Wilson and
406 Butterfield, 2014; Parry et al., 2016; Hou et al., 2017; Slater et al., 2017). As previously
407 mentioned, the overall marginal resolution of the HTP fossils as organic films generally
408 obscures anatomical details, which would be further masked if the cone is tubicolous.
409 However, the regular morphology the HTP fossils may be evidence against tubes, which
410 may be irregular in shape depending on position and integument type (see Meyer et al.,
411 2012 for a longer discussion on tube preservation). Typically benthic priapulids have a

412 ringed body often circled with spines and proboscis ornamented with longitudinal ridges
413 (Liu et al., 2014; Hou et al., 2017; Hu et al., 2017). We did not observe any of these
414 features in the HTP fossils. Polychaetes are segmented worms, which often build
415 biomineralized living tubes and have mineralized teeth, identified as scolecodonts (Rouse
416 and Pleijel, 2001; Hou et al., 2017). Scolecodonts are common and found at some BST
417 localities (Slater et al., 2017), but have not yet been found at the Hummelstown locality.
418 HTP association with either of these groups would seem to require aberrant forms
419 residing in tubicolius cone-like structures and living in the pelagic realm.

420 **CONCLUSIONS**

421 Discovery of exceptionally preserved enigmatic fossils provides a rare glimpse into the
422 character of the Late Ordovician planktic community during the GOBE. The problematica
423 occur as part of a low-diversity assemblage that also includes graptolites and phyllocarids.
424 The fossils appear to have been rapidly buried below the benthic surface after capture in a
425 turbidity event. The flattened graptolites have a fair to good preservation, and the
426 phyllocarid appendages are clearly visible, but without fine detail. The problematica are
427 organic films, generally marginally preserved. The taphonomy of these fossils, especially
428 the presence of framboidal pyrite in association with soft-bodied organic compressions,
429 indicates a Burgess shale-type preservation pathway. The paucity of finely preserved
430 features or internal details may reflect the regional low anchizone metamorphic history of
431 the Martinsburg Formation, which is highly sheared and geologically complex at the
432 collection locality near Hummelstown, Pennsylvania. The phylogenetic identity of the
433 problematica, which consists of a cone-shaped body and external mass, is uncertain (which
434 might include an extinct clade) with suggestions including nominally to non-shelled

435 molluscs, cnidarians, lophophorates, and aberrant priapulid or polychaete worms. The
436 taphonomic factors responsible for the preservation of these fossils merit further study, as
437 we find no evidence of unusual sedimentological conditions at the Hummelstown site. The
438 effects of post-burial (physical and geochemical) metamorphic processes, as they pertain to
439 the Hummelstown locality and BST deposits in general, also merit further consideration.
440 Lastly, it seems significant that the HTP fossils appear unfamiliar given their placement in a
441 time of intense diversification (notwithstanding preservation issues) and unveils a possible
442 association between graptolites and soft-bodied planktic organisms during the GOBE.

443 **ACKNOWLEDGEMENTS**

444 The authors would like to thank the reviewers of previous versions of this
445 manuscript for their insight and suggestions. We would also like to thank the Department of
446 Mineral Sciences at the Smithsonian National Museum of Natural History in Washington,
447 DC for use of their ESEM and facilities that made the analyses in this study possible.
448 Thanks go out to Emma Bullock and Timothy Rose for their help in gaining access, and use,
449 of the analytical equipment at the Smithsonian. Thank you to Arie Janssen and John
450 Repetski for their comments on early drafts of this manuscript. We would also like to thank
451 Gale Blackmer of the Pennsylvania Geological Survey and Elizabeth Graybill for their
452 assistance in the preliminary work on this fossil locale, which was discovered during
453 mapping under grant G09AC00181 from the USGS National Cooperative Geologic
454 Mapping Program. M. B. Meyer and G. R. Ganis carried out field work, J. M. Wittmer (and
455 others) contributed to the interpretation of the fossils. M. B. M, G. R. G., and J. M. W. wrote
456 the paper with input from the other authors.

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744

745

FIGURE CAPTIONS

746 **FIGURE 1**–Geological map of fossil locality. A) Simplified geological map showing the
747 major geologic units and tectonic features around Hummelstown, PA (scale bar = 2 km).
748 Inset shows the location of the state of Pennsylvania on eastern coast of the United States
749 (with the star showing the location of Washington DC). Modified from Blackmer and Ganis
750 (2015). B) Panorama looking west at the outcrop, G. Robert Ganis for scale. C) A close-up
751 of the bedding at the outcrop, rock hammer for scale. D) Image of fossil-bearing slab freshly
752 collected. Weathering has lightened the black shales; pencil for scale.

753

754 **FIGURE 2**–Reflected light, BSE, and EDS imagery of fossil specimens. A) Reflected light
755 image of hand sample containing HTP and graptolite fossils (black arrows). Red arrow
756 points to apex of HTP specimen pictured in figure 3B. (hand sample 700852 pictured). B)
757 Reflected light image of *Diplograptus? foliaceus* (Murchison, 1839) graptolite fossil found
758 in association with the HTP fossils. C) Phyllocarid fossil with a well-defined carapace and

759 segmented abdomen (700849). D) Numerous fossils in association, including *i*)
760 *Amplexograptus* cf. *A. maxwelli*, *ii*) problematica, and *iii*) an unknown fossil (700826).
761 White arrow points to transition from narrower to wider cone-shaped body on problematica
762 specimen. Blue arrow points to possible aperture location. Yellow arrow points to overlap of
763 unknown fossil by problematica specimen (and corroborated by counterpart, not pictured).
764 E) BSE/SEM hybrid image of Fe-oxides, formerly pyrite framboids (hand sample 700852
765 pictured). F) EDS maps of the cone-shaped posterior body area of fossil (700830). Fossil
766 body is between white dashed lines. Scale bars in A–B = 2 mm, C–D = 1 mm, and in E–F =
767 100 μm .

768

769 **FIGURE 3**—EDS maps and reflected light images of HTP and graptolite theca. A)
770 BSE/SEM hybrid image and EDS map composites of graptolite theca (700850). B–C)
771 BSE/SEM hybrid images and EDS maps of HTP (700824). Inset shows location on
772 magnified specimen photo (in same position as in B and C). B) Apex tip. C) Possible
773 external body mass. D–E) *Cryptograptus insectiformis* partially covered by HTP (700851).
774 D) Original image C) Highlighted image, Graptolite (blue) and HTP (green). Scale bars in
775 A–C = 100 μm , D–E = 2 mm.

776

777 **FIGURE 4**—Basic Hummelstown Problematica fossil forms. A) Typical specimen with two-
778 part body plan and clear aperture and external body-mass exhibited (700823). This specimen
779 also displays a ‘spindle’ shape where the cone-shaped posterior body widens, then narrows,
780 as it gets closer to the aperture. *i*) Raw image of specimen. *ii*) Annotated specimen. Black
781 bars indicate extent of external body-mass. Blue arrow denotes intersection of the cone-

782 shaped posterior body and the external body mass. White arrows show pointed features.
783 Dotted white line shows narrowing of the 'spindle' shape and the flared terminus of the
784 cone-shaped body. B) Each row contains (from left to right) a model of the Hummelstown
785 Problematica body construction and preservation next to example fossil specimens. 1)
786 Specimens with only the cone-shaped posterior body (*pb*) preserved (the external body mass
787 may be missing or retracted (1a=700830; 1b=700842; 1c=700829). 2) Specimens with some
788 external body mass (*xbm*) present (possibly partially-retracted) (2a=700839; 2b=700825;
789 2c=700840). 3) Specimens with relatively large amounts of external body mass present
790 (3a=700843; 3b=700845). Blue arrows denote intersection of *pb* and *xbm*. Black arrows
791 point to distinctive narrowing of the body near the posterior apex. White arrows show
792 pointed features. Black brackets indicate extent of external body mass on fossil specimen.
793 Scale bars: A = 3 mm, B = 1 mm.

794

795 **FIGURE 5**—Specimens of Hummelstown problematica, grouped by morphotype; A) Long
796 and narrow, and B) Short and wide. Specimen identification numbers are, for morphotype
797 A: 1=700823, 2= 700824, 3= 700825, 4= 700826, 5= 700827, 6= 700828, 7= 700829, 8=
798 700830, 9= 700831, 10= 700832, 11= 700833, 12= 700834, 13= 700835, 14= 700836, 15=
799 700837, 16= 700838. For morphotype B: 17= 700839, 18= 700840, 19= 700841, 20=
800 700842, 21= 700843, 22= 700844, 23= 700845, 24= 700846, 25= 700847, 26= 700848.

801 Scale bars = 2 mm.

802









