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1 **Evolutionary significance of the blastozoan *Eumorphocystis* and its**
2 **pseudo-arms**

3

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16

17 **Running header:** *Eumorphocystis*, pseudo-arms, homoplasy with crinoids

18

19 **Abstract.**—Twelve *Eumorphocystis* specimens provide the basis for new findings and a more
20 informed assessment of whether this blastozoan (eocrinoids, blastoids, diploporites,
21 rhombiferans) constitutes the sister taxon to crinoids, as has been recently proposed. Both
22 *Eumorphocystis* and earliest-known crinoid feeding appendages express large longitudinal
23 canals, a demonstrable homology exclusive to these taxa. However, the specimen series studied
24 here shows that *Eumorphocystis* canals constrict proximally and travel within ambulacrals above

25 the thecal cavity. This relationship is congruent with a documented blastozoan pattern but very
26 unlike earliest crinoid topology. Earliest crinoid arm cavities lie fully beneath floor plates; these
27 expand and merge directly with the main thecal coelomic cavity at thecal shoulders. Other
28 associated anatomical features echo this contrasting comparison. Feeding appendages of
29 *Eumorphocystis* lack two-tiered cover plates, podial basins/pores, and lateral arm plating, all
30 features of earliest crinoid "true arms". *Eumorphocystis* feeding appendages are buttressed by
31 solid block-like plates added during ontogeny at a generative zone below floor plates, a pattern
32 with no known parallel among crinoids. *Eumorphocystis* feeding appendages express brachioles,
33 erect extensions of floor plates, also unknown among crinoids. These several distinctions point to
34 non-homology of most feeding appendage anatomy, removing *Eumorphocystis* and other
35 blastozoans from exclusive relationship with crinoids. *Eumorphocystis* further differs from
36 crinoids in that thecal plates express diplopores, respiratory structures not present among
37 crinoids, but ubiquitous among certain groups of blastozoans. Phylogenetic analysis places
38 *Eumorphocystis* as a crownward blastozoan, far removed from crinoids.

39

40

41 **Introduction**

42

43 It was suggested long ago that blastozoans (eoccrinoids, blastoids, diploporites,
44 rhombiferans) and crinoids comprise a monophyletic assemblage, the so-called Pelmatozoa
45 (Leuckart, 1846), largely on the basis of common possession of a superficially similar
46 attachment stalk. In spite of doubts about this interpretation that arose during the mid-20th
47 century (Ubaghs, 1953, 1968; Sprinkle, 1973), this canon was perpetuated in major reference

48 works such as the *Treatise on Invertebrate Paleontology* and persists in many publications to the
49 present day. Works seeking to separate blastozoans and crinoids as only distantly related
50 pentaradiate forms or reject the pelmatozoan hypotheses that crinoids and blastozoans share
51 exclusive common ancestry, have met with considerable resistance (Clausen et al., 2009; Zamora
52 and Smith, 2011; Kammer et al., 2013; Sumrall, 2017; Sheffield and Sumrall, 2019a, 2019b;
53 inter alia).

54 However, even detractors of the idea that crinoids and blastozoans are only superficially
55 similar and do not form an exclusive clade seem to have accepted the importance of the crucial
56 suite of feeding appendage features cited by those who question the validity of Pelmatozoa, or at
57 least argue that any resemblances are superficial (Mooi and David, 1998, 2000; David and Mooi,
58 1999; Guensburg and Sprinkle, 2007; Guensburg et al., 2020, inter alia). For example,
59 proponents for blastozoan ancestry of crinoids claimed an unnamed Middle Cambrian blastozoan
60 represented only by disarticulated plates provided evidence that somatocoelar extensions from
61 the main body cavity continued into the arms (Clausen, 2009). However, it is also clear these
62 supposed blastozoan arms lacked any extraxial elements. The purported coelomic canals pass
63 through floor plates toward the peristome, not through the thecal shoulder, which is an anatomy
64 unlike crinoids. The diminutive nature of these blastozoan canals is also problematic. Other
65 workers cited this and other evidence to reject the idea that any canals within the appendages of
66 blastozoans represented spaces for somatocoelar extensions (Guensburg et al., 2010). In spite of
67 attempts to clarify the issue through precise anatomical descriptions, the debate continues. Here,
68 we shed new light on another purported “missing link” between crinoids and blastozoans.

69 Recently, a proposal that *Eumorphocystis multiporata* Branson and Peck, 1940,
70 (hereafter, *Eumorphocystis*, as all specimens are conspecific topotypes), a diplopore-bearing

71 blastozoan, represents the nearest-known sister group to crinoids has been published (Sheffield
72 and Sumrall, 2019). Evidence central to this suggestion, largely derived from a single specimen,
73 is the description of a longitudinal canal within each of this taxon's feeding appendages. These
74 canals are stated to pierce the theca and connect with the thecal coelomic cavity in a manner
75 similar to that known for crinoids (Sheffield and Sumrall, 2019).

76 Two ancillary putative homologies follow: "arm" construction consisting of triserial (here
77 referred to as tripartite, because an aboral series is not in strict one-to-one sequence with the
78 other two) axial and extraxial elements, and the presence of "radial" plates from which an aboral
79 uniserial set of "brachial" extraxial elements extends distally out these appendages. We
80 reconsider and test this proposal using new and existing observations from 12 *Eumorphocystis*
81 specimens. These data are then compared with an expanded update of early crinoid arm
82 morphology recently made available through examination of earliest crinoids. These data have
83 only recently been more fully explicated in the context of crinoid origins (Guensburg et al.,
84 2020).

85 A full understanding of the feeding appendages of *Eumorphocystis* has been a long-term
86 process, and even now some details, such as their full length, remain unknown (Fig. 1). The
87 original description of *Eumorphocystis* (Branson and Peck, 1940) was based on the holotype
88 alone, in which the appendages are broken off close to the theca. This led to the initial
89 conclusion that exothecal feeding appendages were lacking in this taxon. More complete
90 *Eumorphocystis* specimens provided the first evidence of "arms" (Parsley, 1982). Initially, these
91 were considered of blastozoan origin and only homoplastic on crinoid arms (Parsley, 1982).
92 Recently, the discovery that early crinoids express what could also be considered a tripartite
93 pattern (Guensburg and Sprinkle, 2009) formed the basis for a reinterpretation that

94 *Eumorphocystis* “arm” anatomy is homologous to that of early crinoids (Sheffield and Sumrall,
95 2019a). In this paper, however, we add descriptive data and imagery that enhance our
96 understanding of, and provide a basis for, interpretation of *Eumorphocystis* “arms” that is in
97 agreement with the original suggestion that *Eumorphocystis* is of strictly blastozoan affinity
98 (Parsley, 1982). The present data confirm most of the basic “arm” construction details, but reveal
99 significant points of departure, particularly at the juncture of arms to theca (Sheffield and
100 Sumrall, 2019a). This new information forms the core of our reappraisal of the evolutionary
101 significance of *Eumorphocystis*.

102

103 **Repositories, Material, Stratigraphic Occurrence, and Methods**

104

105 Specimens used for this study were selected to provide data concerning feeding
106 appendage and associated thecal anatomy. Virtually no additional preparation beyond that
107 already accomplished was needed. Specimens were photographed using a Leica dms 300 digital
108 camera fitted with stacking capability.

109 *Repositories and institutional abbreviations.*— *Eumorphocystis* specimens used in this
110 study are housed in the collections of the Sam Noble Museum (OU), University of Oklahoma,
111 Norman, and the Non-vertebrate Paleontology Lab (----TX--, NPL) at the University of Texas,
112 Austin. These twelve topotypes are: OU 9047, OU 9048, OU 9049, OU 238156, OU 238157,
113 OU 238158, OU 238159, 1107TX2, 1279TX126, 1279TX339, 1404TX6, and NPL 93144 ([Table](#)
114 [1](#)). We also examined a plaster cast of the holotype, OU 3123. Codings for other taxa used in the
115 phylogenetic analysis were primarily obtained from published sources and checked with

116 specimens in the collections of the Field Museum, Chicago, and the Non-vertebrate Paleontology
117 Laboratory at the University of Texas, Austin.

118 All *Eumorphocystis* specimens were collected from the Lower Echinoderm Zone,
119 Mountain Lake Member, Bromide Formation, Arbuckle Mountains, Oklahoma. Detailed locality
120 data are available from respective repositories. The Bromide Formation is Sandbian, early Late
121 Ordovician, in age.

122

123 **Preservation and Taphonomy**

124

125 Most *Eumorphocystis* specimens were surface collected and largely free from enclosing
126 calcareous shale, but a few are preserved on carbonate grainstone surfaces. Specimens are
127 usually three dimensional or nearly so, with negligible crushing. No specimen preserved with
128 complete feeding appendages or stems is known. Instead, available material consists of thecae
129 with arms broken off at varying distances from the theca. The different breakage patterns are
130 important for tracing features such as those involved in the transition from theca to appendage.
131 Only a few specimens preserve proximal portions of the stem, the longest-known segment with
132 31 “columnals”. Specimens show variable amounts of grainy calcite overgrowths and spar
133 infilling of stereom, presumably the result of rapid post-mortem cementation. This is not a
134 serious impediment for observing anatomy such as thecal plate sutures, but it can obscure details
135 of microscopic structures germane to assessing the features crucial to determining the
136 evolutionary significance of *Eumorphocystis*. In some cases, there are no apparent canals in the
137 thecal or near-thecal portions of the ambulacra. In a few cases, specimens corroded by
138 differential dissolution weathering, presumably resulting from more soluble low magnesium

139 cement versus high-magnesium echinoderm stereom, reveal tiny canals. These are continuations
140 of larger feeding appendage canals. In addition, the twelve specimens available furnish data on
141 intraspecific variation. These findings are incorporated into the subsequent analysis.

142

143 **Character analysis**

144

145 Here we provide new information in the form of a character analysis for features of an
146 admittedly contentious fossil, *Eumorphocystis*. The focus is primarily on feeding appendages but
147 includes observations from adjacent skeletal anatomy as well. This analysis is based on
148 examination of specimens hitherto unexamined by those who have suggested a sister group
149 relationship to crinoids for this taxon (Sheffield and Sumrall, 2019a; Deline et al., 2020).

150 Accompanying reasoning that strongly supports a position for *Eumorphocystis* contrary to this
151 earlier work is presented with this analysis. The cases for or against hypotheses of homology,
152 here and in the opposing viewpoint, both depend upon congruency and accepted ontogenetic,
153 morphological, and positional criteria for homology (Patterson, 1988; Freudenstein, 2005).

154 Past criticisms of our conclusions regarding the origins of crinoids (most recently
155 Sheffield and Sumrall, 2019a) cited reliance on what were perceived to be a priori assumptions.
156 It was claimed that our work presupposed reasoning or knowledge proceeding from theoretical
157 deduction. However, accepted theories such as the Extraxial-Axial Theory were developed from
158 empirical observations and theoretical induction, not the other way around (Mooi and David,
159 1997). Our aforementioned methodology is brought to bear on hypotheses of homology in a
160 detailed explication, without coding based solely on superficial resemblances of individual
161 features that do not fully consider information gleaned from other sources, including but not

162 restricted to the overall relationships of these features one to another. Our approach has, and
163 continues to be, utilization of these explications to code features, and to test these hypotheses of
164 homology in a full phylogenetic analysis. This approach is integral to the uncovering of
165 phylogenetic signal.

166 The same authors criticizing our approach rely on analyses that do not provide detailed
167 delineation of character state parameters, full probing of superficial similarity, or support for
168 why a given transformation series should be a part of a given character or carry phylogenetic
169 signal (Kammer et al., 2013; Sumrall, 2017; Wright, et al., 2017; Deline, et al. 2020; inter alia).
170 Approaches that differ from ours (e.g. Deline et al. 2020) leave uncited available data, or
171 findings that undermine codings they favor (David et al., 2000; Guensburg et al., 2010;
172 Guensburg et al., 2016; Lefebvre et al., 2019; inter alia). We prefer a different way of dealing
173 with echinoderm phylogeny, particularly when working with fossils open to more than one
174 interpretation. As stated in Mooi and David (1997: 306), "The issue of subjectivity versus
175 objectivity is often raised in reference to character analysis, usually with the implication that it is
176 not objective to try to assess the degree to which we can trust phylogenetic signal from certain
177 features. As cladists interested in quality of data as well as quantity, we are resisting the
178 implication that the more we know about our characters, the less objective the study will be."

179 A criticism of our methodology centered on reliance upon differences rather than
180 similarities in our analyses (Wright et al., 2017, p. 831). This oversimplifies our approach and
181 does not fully recognize the strengths of the phylogenetic method itself. Similarities and
182 differences are nested concepts and provide the basis for evaluation of critical issues concerning
183 homoplasy or homology. Commonality at one level of universality will be a difference at
184 another, and our application of the data we have gathered recognize this explicitly. Moreover,

185 our insistence that certain features should not be considered even comparable or coded under the
186 same character system is not founded on a search for differences. We are attempting to address
187 the more profound problem that past nomenclature has reified concepts of similarity that are
188 either inapplicable or violate the central principle that such analyses should capture phylogenetic
189 signal. Our approach employs nuanced and detailed observations drawn from several sources but
190 does not overtly rely on differences. Our evaluations continue to be founded among long
191 established criteria: conjunction, congruence and similarity, and an intimate knowledge of the
192 material at hand (Patterson, 1988; Freudenstein, 2005).

193 We base our characters and codings on analytical data from combined observations
194 accumulated over a period of decades within the framework of established phylogenetic practice
195 (Guensburg, 2012; Guensburg, et al., 2020), and on empirical observations informed by
196 ontogenetic and anatomical information from a wide variety of sources (partially summarized in
197 Mooi and David, 1998; Mooi et al., 2005; inter alia), including from extant specimens whose
198 anatomy is frequently ignored in the context of what is plausible among fossil forms. Recent
199 workers have appropriately applied new or previously little used methodology to the issue of
200 crinoid phylogeny (Ausich, 2015b; Wright et al., 2017), but such approaches should incorporate
201 information from other well-founded methodologies including those utilized here and in other
202 works (e.g. Guensburg et al., 2016; Guensburg, et al., 2020).

203 Here, we start with observations benefiting from anatomical details furnished by the large
204 *Eumorphocystis* sample size, improved understanding of earliest crinoid morphology and data
205 from origins of specific body wall regions (Mooi and David, 1997, 2008; David et al., 2000;
206 Guensburg and Sprinkle, 2007, 2009; Guensburg, 2012; Guensburg et al., 2016; Guensburg et
207 al., 2020; inter alia). We begin with the three homologies proposed to link *Eumorphocystis* to

208 crinoids (Sheffield and Sumrall, 2019a) and continue with expanded comparative data from
209 feeding appendages and beyond. These ultimately test the number and specific kinds of
210 transformations in a series of hypothetical evolutionary events required to support an exclusive
211 link between *Eumorphocystis* and the common ancestor of Crinoidea.

212

213 *Coeloms*.—The central issue and a principal point of departure of the concept that crinoids are
214 sister to *Eumorphocystis* (Sheffield and Sumrall, 2019a) in this restudy concerns the
215 interpretation of canals associated with feeding appendages. Adding uncertainty to this matter is
216 the scarcity of comparative information for brachiolar and floor plate canals of blastozoans in
217 general (see Sprinkle, 1973; Clausen et al., 2009, for examples). Among early crinoids, these
218 data have only recently been extensively analyzed in a phylogenetic context, although the nature
219 of these canals has long been understood from an anatomical standpoint (Heinzeller and Welsch,
220 1994; and summarized in Guensburg et al., 2020).

221 Present evidence shows that longitudinal feeding appendage canals, otherwise termed
222 median canals (Sprinkle, 1973), exist in a diversity of blastozoans (gogiids, rhipidocystids,
223 rhombiferans, blastoids) (Fay, 1960; Sprinkle, 1973; 1975; Clausen, et al., 2009; Sumrall and
224 Sheffield, 2019a) (Figs 2-4, 6.1-6.4, 6.6, 6.8, 6.9). However, the generally small scales of
225 available material, and the tendency for diagenesis to obscure details with calcitic infilling or
226 eliminate them through moldic preservation that show only plate exteriors, combine to contribute
227 to the scarcity of data. Further, material with attached feeding appendages remains unavailable
228 for many blastozoans, and even ambulacra on thecae are not commonly broken through in such a
229 way that might reveal internal canals. Not surprisingly, no comprehensive study of blastozoan
230 median canals is available, and none is documented for most taxa. Blastozoan median canals

231 pass through floor plates and their extensions, the brachiolars, presumably to their tips. They are
232 housed within floor plates, and in nearly all known cases, pass between opposing floor plate
233 elements along the appendage mid-line. In one case, canals are encased in uniserial floor plates
234 extending from arms to the theca (Clausen, et al., 2009). Position of canals and the fact that these
235 seem to extend to the oral region suggest they housed nerve branches extending from the
236 circumoral ring. This latter anatomical configuration can be observed among living echinoderms.

237 Previously reported blastozoan canals are circular openings, on the order of 0.1 mm^2
238 (using $A = \pi r^2$, the area for a circle) or smaller in section. These are housed within floor plates
239 or, in the case of brachiole-bearing blastozoans, brachiolars. The roughly elliptical appendage
240 cavities seen in *Eumorphocystis* are larger than those of other blastozoans, being approximately
241 1.3 mm^2 in section (using $A = \pi ab$, the area for an ellipse) (Fig. 2.2, but see Fig. 3.6 for much
242 smaller canal). These transition proximally to much smaller, more circular, canals,
243 approximately 0.14 mm^2 in section (Figs. 3.2, 3.4-3.6, 4.2, 4.6), on a scale similar to those of
244 other blastozoans. These small proximal canals are often obscured by spar-filling similar in color
245 to adjacent spar-filled plates (Figs. 2.3, 3.4, 4.1). This narrowing occurs at the second to fourth
246 ambulacrals distal to the orals, except in the C-ray where differentiated floor plates skirt the
247 periproct region. In both cases, though, this change takes place not far beyond the thecal wall.
248 Topology in the proximal regions agrees with the most common blastozoan pattern in that canals
249 run along the perradial sutures (ambulacral midline) that form contacts between opposing floor
250 plates. On the theca itself, canals proceed within floor plates just above, but not through, the
251 thecal wall (Figs. 4.2, 4.3). These narrow canals were observed to reach the orals (Fig. 3.5).
252 Opposing floor plate walls each form a hemi-canal or “half-pipe” (Fig. 3.2, 3.5). Larger than

253 usual more distal canals could have accommodated expanded innervation of appendages
254 supplying the dense array of brachioles.

255 The situation among early crinoids (see Guensburg et al., 2010; Guensburg et al., 2020,
256 for detailed analysis) (Figs. 5, 6.5, 6.7) is not comparable to that of *Eumorphocystis* or any other
257 blastozoan (see Guensburg et al., 2020, for detailed analysis) (Figs. 6.5, 6.7). Unlike blastozoans,
258 crinoid canals expand into the main body mass at thecal shoulders away from the peristome
259 (Figs. 5.1-5.3). In addition, arms themselves express secondary longitudinal grooves within the
260 adoral brachial canals that extend out the arms. Subsequent evolutionary events led to the
261 submergence of this secondary groove into brachials, thereby transforming what initiated as
262 grooves into intraplate canals. Instances of the enclosed canal condition are known from as early
263 as the Late Ordovician (e.g. *Columbicrinus*) (Guensburg et al., 2020, Fig. 7) and occur among all
264 living crinoids. These canals house the brachial (also known as the aboral) nerve, part of the
265 subepithelial system sensu Heinzeller and Welsh (1994). Ontogeny of living crinoids
266 recapitulates this change in position of the nerve canal, which was originally only partly
267 submerged into brachials.

268 It is important to note that the derived brachial canal condition in modern crinoids and
269 certain fossils superficially resembles the situation found among blastozoans. In both cases, a
270 canal perforates the primary skeletal support elements of feeding appendages. However,
271 comparative study of the nature and origin of the plate bearing canals using earliest crinoid as
272 well as modern crinoid anatomy reveals fundamentally different housing elements: extraxial
273 brachials in crinoids, axial floor plate and brachiolar canals in blastozoans (Fig. 6). Accordingly,
274 proposed homology of *Eumorphocystis* feeding structures with those of crinoids becomes more
275 conjectural, since there remains no plausible evidence for somatocoels. The polarity of the

276 changes above does not rely on a priori reasoning, but on reciprocal illumination of direct
277 observation of conditions that have nothing to do with the nerve canals themselves, and that are
278 congruent with the topology of the same tree that makes sense of these canal character
279 transitions.

280

281 *Tripartite pseudo-arms*.— See *Summary of character analysis findings* below for definition of
282 "pseudo-arm". A finding for homologous tripartite feeding appendages assumes this condition
283 arose through the blastozoan *Eumorphocystis* to be inherited by earliest crinoids. Recently
284 revealed evidence from earliest crinoids does not support such a series of events because the
285 tripartite pattern is not the earliest condition for crinoid arms (Guensburg et al., 2020). Instead, it
286 simply represents an additional state observed among more crownward crinoids, a state not
287 found among the common ancestor of that group. Earliest crinoid arms (*Apektocrinus*,
288 *Titanocrinus*, *Glenocrinus*) are not tripartite because they express lateral fields of platelets
289 extending from the cup along the arms between brachials and floor plates, in one case, all the
290 way to the arm tips (e.g. *Titanocrinus*) (Guensburg et al., 2020, Figs. 10.5, 10.6).

291

292 *Radials*.—Differentiated thecal plates lying at the base of the extraxial feeding appendage
293 series in *Eumorphocystis* have been interpreted to be homologous with similarly positioned
294 crinoid radials (Sheffield and Sumrall, 2019a). These, like those of crinoids lie at the base of a
295 uniserial, radially positioned plate column, occur at the juncture with the thecal wall, and express
296 a distinct facet articulating with a more distal extraxial plate. The comparison of proposed
297 *Eumorphocystis* radials fails when a more nuanced attempt to homologize this pattern with that
298 of Early Ordovician crinoids is implemented. In early camerates (Guensburg and Sprinkle,

299 2003), fixed brachials continue upward from radials in a uniserial series within the body wall.
300 However, in the case of *Eumorphocystis*, no uniserial body wall plates continue above putative
301 radials (*Eumorphocystis backing series* below). If the comparison is with cladids, the radial
302 facets should express notches accommodating the passage of coeloms extending outward from
303 the thecal shoulder, yet they do not. There is no opening leading distally into the feeding
304 appendages from the “radials” of *Eumorphocystis*. Plates extending distally from the proposed
305 *Eumorphocystis* “radial” confirm this anatomy. The first aboral plate beyond the “radial” of
306 *Eumorphocystis* lacks an adoral groove. Stated another way, the proposed coelomic canal
307 (above) does not bound either the putative radials or in the first two or three subsequent putative
308 brachials. Furthermore, diplopores are evident in the so-called radials in *Eumorphocystis* (Fig.
309 2.6), features unlike crinoid respiratory structures.

310
311 *Ambulacral grooves*.—Ambulacral grooves of *Eumorphocystis* are narrow and shallow,
312 approximately only a quarter of the entire arm width. Those of early crinoids are wide and deep,
313 set down within the adoral grooves of brachials, spanning the entire floor plate and arm's width.
314 It is not until more crownward taxa within the Crinoidea that narrower ambulacral grooves are
315 encountered. It is unparsimonious to hypothesize that *Eumorphocystis* represents the
316 plesiomorphic morphology of the common ancestor of crinoids and blastozoans when the earliest
317 crinoids express dissimilar groove morphology, only to see something similar reappear in
318 crownward crinoids, particularly when an alternative more parsimonious placement of
319 *Eumorphocystis* exists.

320

321 *Floor plates.*—Like blastozoans in general, *Eumorphocystis* floor plates are massive, blocky
322 elements lacking podial pores. They have large exposed surfaces, both on the theca, and along
323 pseudo-arms, where they form the exposed tops and sides of arms. In nearly all blastozoans,
324 pseudo-arms do not include extraxial elements and form the entire aboral appendage surface.
325 Each *Eumorphocystis* floor plate bears a facet that facilitated infolding of an attached brachiole
326 toward the peristome (Figs. 2.1, 2.4). The initial floor plate just beyond the orals is distinctly
327 elongate. By contrast, early crinoid floor plates are delicate, largely internal, slat-like elements,
328 with shared podial pores between sequential elements (Guensburg and Sprinkle, 2001, 2009;
329 Guensburg et al., 2020). Arm support in this case is provided by brachials, the extraxial elements
330 that form the aboral surface of the arm (Fig. 5). Although one could envision that thin crinoid
331 floor plates were highly modified from the block-like versions seen in *Eumorphocystis*, the lack
332 of podial pores makes this an unparsimonious proposition given the frequency of pores in other
333 echinoderms (e.g. edrioasteroid-like forms, certain edrioasteroids) that have hitherto not at all
334 been at all associated with blastozoans. In other words, extensive convergent evolution of podial
335 pores would have to be proposed in the face of strong similarities among them, as well as
336 broadly accepted phylogenetic evidence supporting blastozoan monophyly to the exclusion of all
337 other major echinoderm clades (Guensburg et al., 2016; Guensburg et al., 2020).

338

339 *Pinnules and brachioles.*—First, it should be recognized that blastozoan brachioles and crinoid
340 pinnules, although superficially similar, are only partly homologous structures in which
341 respective nonhomologous portions indicate significantly different soft tissue anatomies. Both
342 crinoids and blastozoans express cover plates, axial constructs over the ambulacra. However,
343 primary supporting skeletal structures are non-homologous. Blastozoan brachiolar are axial

344 extensions from ambulacral floor plates, crinoid pinnulars are extraxial extensions from the
345 thecal body wall beyond the ambulacra (Mooi and David, 1997, 1998). Brachioles were a
346 diagnostic blastozoan apomorphy from the onset of their origination during the Early Cambrian
347 (Sprinkle, 1973). On the other hand, all known earliest crinoids were apinnulate (Guensburg,
348 2012; Guensburg et al., 2020). It is widely agreed among crinoid workers that pinnules evolved
349 independently at different times among camerate, cladid, and disparid crinoids (Ausich, 1988;
350 Sheffield and Sumrall, 2019a). Modern crinoid anatomy shows the same basic anatomy in arms
351 and pinnules including the presence of left and right somatocoel extensions (Mooi and David,
352 1997, 1998). There is no evidence that would support a different conclusion in the various fossil
353 crinoids.

354 Thecal and feeding appendage floor plates of *Eumorphocystis* each bear a uniserial
355 brachiole (Fig. 2.1). These formed a dense filtration fan superficially much like pinnulate crinoid
356 arms (Parsley, 1982) (Fig. 1). The suggestion that a *Eumorphocystis*-like ancestor first lost
357 brachioles, then later evolved pinnules, after crinoids themselves had evolved (Sheffield and
358 Sumrall, 2019a) , requires loss of brachioles in a pre-crinoid phase, followed by development of
359 pinnules after the origination of crinoids. The added complexity for this posited sequence of
360 events undermines supposed homology between the feeding appendages of *Eumorphocystis* and
361 the arms of any of the pinnulate crinoids, whether pinnules evolved more than once or not.

362
363 *Cover plates.*—Arm cover plates of earliest crinoid are arranged in a two-tiered pattern
364 (Guensburg et al., 2020). *Eumorphocystis* appendage cover plates are arranged in a single-tiered
365 alternating biseries, each with a transverse keel running laterally or orthogonal to the longitudinal
366 axis of the appendage (Fig. 2.1). This biseries pattern occurs consistently among early blastozoan

367 brachioles (e.g. the Cambrian imbricates such as lepidocystids, and gogiids) (Sprinkle, 1973).
368 Ambulacral and oral surface cover plating can be more complex, an irregular multi-series,
369 usually a biseries, within a single tier. Derivation of a two-tiered early crinoid-type cover plate
370 pattern from this single blastozoan biseries necessitates novel development of additional plates in
371 stories. Accordingly, this option is not parsimonious given that complex cover plate
372 configurations from which an incipient two-tiered early crinoid pattern potentially originated
373 were available among Cambrian edrioasteroid-like (Smith and Jell, 1990, Fig. 4a; Zhao et al.,
374 2010, Fig. 6.7, for instance) and Early Ordovician edrioasterid edrioasteroid (Sprinkle and
375 Sumrall, 2015; Zamora et al., 2015, et al.) echinoderms (see Guensburg et al, 2020).

376

377 *Eumorphocystis backing series*.—Exterior views of the uniserial backing plates of
378 *Eumorphocystis* appear crinoid-like. However, their interiors (oral surfaces) do not. The adoral
379 groove of early crinoids is much larger and deeper than the groove forming the bottom of the
380 pseudo-arm canal in *Eumorphocystis* and in crinoids, it bears a secondary groove (Figs. 6.4, 6.5
381 and 6.7).

382

383 *Pseudo-arm buttressing*.—*Eumorphocystis* pseudo-arms are buttressed by a solid wedge of
384 plates underlying floor plates. Additions to this plate wedge are inserted below floor plates
385 during ontogeny. Crinoid arms expand approaching the theca and this expanded region is hollow,
386 the expanding space bounded aborally by brachials and thin lateral plate fields that lie just
387 aborally to the floor plates (Figs. 5, 6.5, 6.7). No known intermediaries link these disparate
388 morphologies.

389

390 *Summary of character analysis findings.*—Detailed anatomical analysis does not support
391 somatocoelar, radial, or brachial homologies linking *Eumorphocystis* with crinoids. To signify
392 these essential differences between the feeding appendages in blastozoans, and the “true arms” of
393 crinoids, we refer to those seen in *Eumorphocystis* and other blastozoans with similar
394 configurations as “pseudo-arms” (referred to as exothecal ambulacra by Sprinkle, et al., 2011).
395 Thecal plate and respiratory systems, and stem/stalk morphology concur with these findings
396 (Guensburg and Sprinkle, 2007; Guensburg et al., 2010; Guensburg et al., 2016).

397

398 **Testing the claim of crinoid sister-group status for *Eumorphocystis***

399

400 The finding for a sister group relationship of *Eumorphocystis*, a blastozoan, and crinoids
401 was accompanied by a phylogenetic analysis (Sheffield and Sumrall, 2019a). A more recent
402 study that used *Eumorphocystis* and other taxa from this study, recovered different results – that
403 crinoids arose independently from pentaradiate echinoderms apart from blastozoans (Guensburg
404 et al., 2020). The present analysis builds upon this latter study, with a primary goal to elucidate
405 further the phylogenetic position of blastozoans, and in particular *Eumorphocystis* within this
406 context. The total taxon list from Guensburg et al. (2020) is expanded from 21 to 25 (Table 2),
407 and the character list increased from 34 to 39. Essentially the entire range of taxa used to support
408 a *Eumorphocystis* sister-group status with crinoids was implemented (Sheffield and Sumrall,
409 2019a). Added taxa include a Middle Ordovician hemicosmitid, a Silurian coronoid blastozoan,
410 and a diplobathrid crinoid. Furthermore, we included the Early Ordovician rhodocrinitid
411 *Proxenocrinus*, among the earliest-known pinnulate crinoids. However, Cambrian and Early

412 Ordovician taxa continue to remain in the overall taxon list in order to code for characters found
413 in the earliest members of the clades to which they belong.

414

415 1. *Left and right somatocoels*: left and right somatocoels underlie ambulacra along their
416 entire length (0); somatocoels restricted to thecal interior (1). State (0) includes those
417 arm-bearing taxa with cavities extending uninterrupted from thecal shoulders. This trait,
418 from a practical standpoint, highlights a key difference in feeding appendage
419 construction. State (1) includes cases where cavities do not extend uninterrupted from the
420 theca, such as *Eumorphocystis*. Here, this relationship is considered similar to that of
421 paracrinoids where such a cavity has been referred to as a lumen (Parsley and Mintz,
422 1975).

423 2. *Podial pores or basins*: present (0); absent (1). Determining the existence of podial
424 pores or podial basins is crucial to assessing relationships among early crinoids, as well
425 as with other early echinoderm groups. The fossils can be difficult to interpret where
426 weathering and diagenesis obscure plate boundaries such as in the fossils treated here
427 (see *Taphonomy and Preparation* above). The best supported interpretation, obtained by
428 coated, submersed, and dry images, is that there are at least podial basins if not actual
429 pores in basins that extend to water vascular elements inside the coelom, internal to the
430 floor plates. Although not documented in later Paleozoic crinoids, these structures can
431 be seen in *Aethocrinus*, *Athenocrinus*, *Apektocrinus*, *Titanocrinus*, and possibly
432 *Glenocrinus* (Guensburg et al., 2020, Figs. 4.4, 4.6, 10.3, 10.4).

433 3. *Floor plates on the theca*: floor plates short, relatively wide (0); long, relatively narrow
434 (1). This trait does not code for appendage morphology.

- 435 4. *Floor plates in appendages*: plates thin, slat-like, not providing primary appendage
436 supports (0); thick, blocky, forming primary appendage skeletal supports (1).
- 437 5. *Ambulacral cover plates*: arranged in lateral and medial tiers (0); in a single biseries of
438 lateral plates (medial tier not expressed) (1). Medial and lateral tiers were previously
439 referred to as primary and secondary cover plates (Paul and Smith, 1984). Single cover
440 plate tiers can be arranged in an alternating double or other multiple series, but
441 essentially forming one level. This differs from the two-tiered pattern where cover
442 plates form two distinct levels (Guensburg et al., 2020). Patterns can be difficult to
443 interpret in plesiomorphic Cambrian forms where plates are more irregular, but an
444 incipient two-tiered pattern can be discerned (Smith and Jell, 1990; Zhao et al., 2010).
- 445 6. *Medial cover plates*: overlapping elements diminishing in size as they arch over the
446 perradial suture (0); an alternating double biseries (1). This character requires medial
447 cover plates and is scored as inapplicable for those taxa lacking medial cover plates.
- 448 7. *Hinging of thecal (non-appendage) cover plates*: hinged, capable of opening and
449 closing (0); fixed, forming closed ambulacral tunnels (1).
- 450 8. *Axial orals*: absent (0); expressed as differentiated interrarial elements surrounding the
451 peristome in all interrays and forming junctions of ambulacra (1). Axial orals are not
452 regarded as homologous with similarly positioned, extraxial, oral-like plates such as
453 those of modern crinoids or of *Hybocrinus nitidus* and *Carabocrinus treadwelli* (see
454 Guensburg et al, 2016, for supporting argumentation). Further, earliest hybocrinids lack
455 orals entirely, suggesting acquisition independent from (and therefore not homologous
456 with) the orals seen in blastozoans such as *Eumorphocystis* (Guensburg and Sprinkle,
457 2017). The plating of the oral region of *Stromatocystites pentangularis* includes oral-

458 like plating in AB and EA interrays. This latter state is autapomorphic among the taxa
459 studied and is omitted from the analysis.

460 9. *Brachioles*: absent (0); present (1). Brachioles are entirely axial in construction
461 whether uniserial or biserial, their primary support structures always arising from
462 (axial) floor plates, or representing extensions of those floor plates beyond the
463 perforate extraxial region.

464 10. *Fixed rays*: contacted entirely by non-standardized plating (0); contacted by standardized
465 circlet(s) in part or entirely (1). Fixed rays are the uniserial series in continuity with the
466 primary appendage support plate series. This character is inapplicable for those taxa
467 lacking true arms sensu David and Mooi (1999:2) and David et al. (2000: 354)

468 11. *Respiratory pores*: epispines (0); absent (1); diplopores (2). State (1) includes taxa with
469 thin, often corrugated, stereom at plate corners.

470 12. *Thecal base circlet*: absent (0); several irregular plates (1); five infrabasal plates (2);
471 four plates (3); single fused element (4); three plates (5). State (1) consists of a ring of
472 larger thecal plates above a narrower, pinched, pedunculate zone.

473 13. *Dorsal cup*: conical (0); bowl-shaped (1). The term “dorsal cup” requires left and right
474 somatocoels extending from the thecal shoulders (character 1 above). This character is
475 inapplicable for those taxa lacking true arms according to David and Mooi (1999: 92)
476 and David et al. (2000: 354) (see character 19).

477 14. *CD interradius elevation*: not expressed except for periproct or anal cone (0); long
478 cylindrical sac (1).

479 15. *CD interradiial gap plate*: present (0); absent (1). This character requires the presence of
480 true arms. State (0) requires extension of the CD interray gap to the stem/stalk, that is,

- 481 they interrupt the cup base circlet. Gap plates are relatively small and are inserted
482 between an otherwise more or less regular thecal base circlet (character 12).
- 483 16. *True basals*: absent (0); expressed as a differentiated mid-cup circlet between infrabasals,
484 if present, and true radials (1). State (1) requires the presence of true arms and is therefore
485 marked as not applicable in cases when true arms are absent (see character 19).
- 486 17. *Secondary median groove*: absent (0); expressed in feeding appendages (1). State (1)
487 refers to a subsidiary channel along the interior aboral surface of the presumed
488 coelomic channels in feeding appendages and extending from the theca. This groove
489 could have housed the brachial nerve.
- 490 18. *True radials*: absent (0), present (1). A true radial represents the proximalmost extraxial
491 plate of a true arm ray series. These support free arms at least early in ontogeny. This
492 character requires the presence of true arms and is therefore marked inapplicable in
493 cases where true arms are absent. *Eumorphocystis* expresses extraxial elements
494 superficially similar to true radials of the type seen in derived crinoids where radials
495 form the cup top. Unlike crinoids, the *Eumorphocystis* plates are not located at the cup
496 top (see Sheffield and Sumrall, 2019a) and facets have no coelomic notches or other
497 evidence of any communication to the thecal interior.
- 498 19. *Left and right somatocoels extended off the theca in feeding appendages, thus forming*
499 *true arms*: absent (0), present (1)
- 500 20. *True arm branching pattern*: true arms atomous, non-branching (0); isotomously
501 branching (1); endotomously branching (2). This character is scored inapplicable for
502 taxa lacking true arms and refers to distalmost branching pattern.

- 503 21. *Brachials*: absent (0); brachials present (1). Brachials, when expressed, constitute
504 primary skeletal supports for the feeding appendages. This character requires true arms
505 and is scored inapplicable for taxa lacking true arms. *Eumorphocystis* expresses uniserial
506 backing plates superficially resembling brachials, but these do not form primary
507 appendage supports and do not contain a through-going coelomic canal.
- 508 22. *Extraxial laterals*: present, accompanying extended thecal wall out arms (0); absent.
509 Extraxial laterals, when present, occupy aboral arm surfaces aside from brachials. State
510 (0) requires true arms and is scored inapplicable for taxa lacking true arms.
- 511 23. *Platelet webs at branchings*: present (0); absent (1). These plate fields are most
512 parsimoniously regarded as extensions of extraxial lateral plating (see character 22).
513 This character requires true arms and is scored inapplicable for taxa lacking true arms.
- 514 24. *Fixed brachials*: present (0); absent (1). Fixed brachials are ray plates that extend
515 aborally from true radials and are embedded in the cup; they articulate laterally with
516 interradial plates. This character requires true arms and is scored inapplicable for taxa
517 lacking true arms.
- 518 25. *Cup-like fixed brachials*: three or more in all rays (0); none to two in all rays (1); cup-
519 like fixed brachials in C or E rays only (2). Cuplike indicates plates embedded in the cup
520 with margins flush with adjacent cup plates, much like radials. This character requires
521 true arms and is therefore scored inapplicable for taxa lacking true arms. Polarity is
522 established by the known crinoid record.
- 523 26. *One or more brachial pairs in lateral union above branchings*: present (0); absent, not
524 paired above branchings (1). This character requires true arms and is therefore scored
525 inapplicable for taxa lacking true arms.

- 526 27. *Interradial plate fields separating multiple fixed primibrachials*: much wider than fixed rays
527 (0); interradial fields not as wide as fixed rays or absent (1); interradial plate fields absent
528 (2). Width is assessed across the widest portion of the field and compared with the widest
529 fixed brachial. This character requires true arms and is therefore scored inapplicable for
530 taxa lacking true arms.
- 531 28. *CD interradius*: CD interradius extending downward to the base of the thecal cavity
532 (0); ending at true radials (1). State (0) indicates the radial circlet is interrupted across
533 the CD interradius, and state (1) indicates radials are contiguous below the CD
534 interradius. This character requires true arms and is therefore scored inapplicable for
535 taxa lacking true arms.
- 536 29. *Radianal(s) and anal X plates*: absent (0); present (1). State (1) consists of
537 differentiated plates occupying the space below and to the left of a “raised” C radial.
538 The radianal can be absent in later more derived taxa, but not those treated here. States
539 (0) and (1) require presence of true arms and are therefore scored as not applicable for
540 those forms lacking them.
- 541 30. *Anibrachial plate*: absent (0), or present (1). This character requires true arms and is
542 therefore scored inapplicable for those taxa lacking true arms.
- 543 31. *Peduncle, stem, or stalk*: absent or only slightly developed as attachment structure (0);
544 anisotropic, imbricate, plated peduncle (1); irregularly tessellated peduncle with
545 pinched demarcation at base of theca (2); monomeric (holomeric) stem (3); pentameric
546 stalk (4). *Carabocrinus treadwelli* and *Hybocrinus nitidus* pentameres are
547 inconspicuous (see Sprinkle, 1982a, Figs. 45D, 46H). Note: The presence of a stem has
548 traditionally been used as a key feature linking blastozoans and crinoids, together these

549 comprising the pelmatozoans. Stems are now known among edrioasteroids as well as
550 blastozoans and crinoids (Guensburg and Sprinkle, 2007; Guensburg et al., 2010).
551 Therefore, it is not unparsimonious to assume that stems/stalks evolved more than once.
552 Here we identify types of stems where, at least among treated taxa, a pattern emerges
553 whereby blastozoan and earliest crinoid stems are distinguishable. This approach does not
554 apply to later, more crownward taxa where homoplasy presumably results in more similar
555 constructs.

556 32. *Stalk/stem lumen*: absent (0); round or irregular trilobate in cross section (1); pentalobate
557 in cross section (2). This character requires a stalk or a stem and scored as not
558 applicable for those forms lacking a meric stalk/stem.

559 33. *Ray length on theca*: long, approaching the perforate/imperforate boundary in extraxial
560 body wall (0); short, restricted to the region around peristome and not approaching
561 boundary between perforate and imperforate extraxial body wall (1).

562 34. *Extraxial "orals"*: absent (0); present (1). The interradial circlet bordering the
563 peristome of *Hybocrinus nitidus* and *Carabocrinus treadwelli* is considered extraxial
564 and homologous among these and a few other cyathocrinine crinoids (*Porocrinus*,
565 *Palaeocrinus*, inter alia); these are all characterized by flat tegmens of few plates and
566 with a hydropore within a single posterior "oral".

567 35. *Gonopore*: undifferentiated from hydropore (0), a slit-like pore apart from hydropore (1).
568 State (1) requires an opening in the CD interray separate from the hydropore.

569 36. *Hydropore or combined hydropore-gonopore*: an interplate pore bordered by small
570 platelets (0); a slit shared across two plates separate from hydropore (1); an intraplate
571 pore (2), subcircular pore shared across two plates (3).

572 37. *Pinnules*: absent (0), present (1). This character requires true arms. Pinnules are
573 supported by extraxial elements, and are constructed nearly identically to true arms,
574 including containment of coeloms characteristic of arms. Pinnules are not homologous
575 with brachioles, which can nonetheless superficially resemble pinnules.

576 38. *Ray branching in dorsal cup*: no branching in dorsal cup (0); branching from fixed
577 brachial on the theca (1).

578 39. *Uniserial posterior plate column*: absent (0); present (1).

579 These 39 characters were assembled for scoring using Mesquite Version 3.2 (build
580 801), and the nexus file run on PAUP 4.0a (build 167) for Macintosh. All characters were
581 unordered and unweighted; one character was parsimony uninformative ([Table 3](#)). The analysis
582 employed the branch and bound algorithm, consensus trees were computed, and a bootstrap
583 analysis of 10,000 replicates was run using a fast heuristic search.

584

585 **Results of the phylogenetic analysis**

586

587 We are acutely aware that merely piling up evidence that crinoids are different from
588 blastozoans is insufficient to falsify the idea that crinoids are derived from within the blastozoan
589 clade, let alone the diploporites, which appear to be non-monophyletic in any case (Sheffield and
590 Sumrall, 2019b). However, unlike previous analyses, we allow for the strong likelihood that
591 morphologies in feeding and other structures are merely superficially similar in blastozoans and
592 crinoids, and lack phylogenetic signal due to homoplasy. For us, the key to uncovering this
593 homoplasy is detailed study of the fossils themselves, details, in addition to broader comparisons
594 with early taxa of both crinoid and blastozoan clades in which these features have very different

595 expressions from those in more crownward forms. Even if it could be shown that
596 *Eumorphocystis* was a sister to crinoids, this is insufficient to place Crinoidea within any more
597 inclusive blastozoan taxon, without trying to explain why crinoids lack so many of the
598 apomorphies of blastozoans, as also discussed in Guensburg et al. (2020).

599 Nevertheless, our study of material adequate to close data gaps evident in the Sheffield
600 and Sumrall (2019) analysis are not consistent with the suggestion that *Eumorphocystis* is
601 relevant to the question of crinoid relationship with blastozoans. The latter is a monophyletic
602 assemblage exclusive of the Crinoidea. No blastozoans, let alone the highly derived
603 *Eumorphocystis*, are more closely related to crinoids than they are to other blastozoans (see
604 Sheffield and Sumrall, 2019b, for a recent treatment of diploporites, in which *Eumorphocystis*
605 has traditionally been included).

606 Results generally mirror those of Guensburg et al., 2020, and even with additional taxa,
607 and are not surprising given the disparate morphological interpretations relative to those of the
608 opposing view (Sheffield and Sumrall, 2019a). This phylogenetic analysis recovered 660 most
609 parsimonious trees of length 75, consistency index (CI) of 0.675, retention index (RI) of 0.845,
610 rescaled consistency index (RC) of 0.594, and homoplasy index (HI) of 0.307. Strict 50% and
611 majority rule consensus trees are shown in Figure 7, along with the results of the bootstrap
612 analysis. *Eumorphocystis* branches high in the blastozoan lineage, distantly related to crinoids,
613 which are place closer to the earliest pentaradiate echinoderm branch. Blastozoan history
614 begins during the Early Cambrian, separate from crinoids.

615 Crinoids are first recognized during the Early Ordovician (Guensburg and Sprinkle,
616 2003, 2009, inter alia). Arm morphology in both modern and fossil crinoids indicates an origin
617 from non-blastozoan pentaradiate echinoderms (David and Mooi, 1999; Mooi et al., 2000;

618 Guensburg and Sprinkle, 2007; Guensburg et al., 2010; Guensburg et al., 2012; Guensburg et
619 al., 2016; Guensburg et al., 2020). Incorporation of the camerate crinoid taxa *Proxenocrinus*
620 and *Gaurocrinus* in the expanded dataset here (characters 35-39) produced a different overall
621 crinoid topology from an earlier iteration (Guensburg et al., 2020) with disparid and traditional
622 camerate clades as sister taxa. This result contrasts with recent findings (Ausich et al., 2015a;
623 Ausich et al., 2015b; Ausich et al., 2020; and Ausich et al., 2020) but is essentially that
624 suggested by another author (Gahn, 2015). The inclusion of pinnulation, character 37, is
625 interesting because it appears to provide phylogenetic signal only early in crinoid history. This
626 character eventually occurs in disparids and cladids as well as camerates, but the current record
627 indicates this feature evolved first among camerates, during the Late Floian. Pinnules are not
628 known not among cladids and disparids until the Late Ordovician.

629

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634

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820

821 **Table 1.** *Eumorphocystis* specimens studied, with sizes of specimens, and comments on image
 822 orientations used in this study.

823

Specimen number	Thecal height (mm)	Images used
OU holotype cast 3123	50	not illustrated
OU 9047	9.5	A ray 2 nd broken floor plate left, 1 st on right
OU 9048	20	E ray, 1 st floor plate left, 2 nd on right
OU 9049	21	oral surface, C ray hemi-canal
OU 238156	11	not illustrated
OU 238157	29	A ray weathered, 3rd floor plate, stem facet
OU 238158	34	not illustrated
OU 238159	14	not illustrated
1107TX2	-	? ray, 4 th floor plate from oral
1279TX126	28	oral surface, AB oral, B ray hemi-canal
1279TX339	7.5	not illustrated
1404TX6	22	C, weathered, 3 rd floor plate
NPL 93144	-	thecal wall and two pseudo-arm stubs

824

825 **Table 2.** List of taxa used in the phylogenetic analysis (expanded from Guensburg et al., 2020):

826

827 Basal pentaradiate echinoderm

828 *Stromatocystites pentangularis* Pompeckj, 1896

829 *Kailidiscus chinensis* Zhao, Sumrall, Parsley and Peng, 2010

830 *Camptostroma rodgyi* Ruedemann, 1933

831 '*Totiglobus*' *lloydi* Sprinkle, 1985

832 *Pseudedriophus guensburgi* Sprinkle and Sumrall, 2015

833

834 Blastozoans

835 *Kinzercystis durhami* Sprinkle, 1973

836 *Lepidocystis wanneri* Foerste, 1938

837 *Eumorphocystis multiporata* Branson and Peck, 1940

838 *Gogia kitchnerensis* Sprinkle, 1973

839 *Hemicosmites pocillum* Jaekel, 1899

840 *Macrocystella mariae* Callaway, 1877

841 *Rhopalocystis destombesi* Ubaghs, 1963

842 *Stephanocrinus gemmiformis* Conrad, 1842

843

844 Stylophorans

845 *Ceratocystis perneri* Jaekel, 1901

846

847 Crinoids

- 848 *Aethocrinus moorei* Ubaghs, 1969
- 849 *Alphacrinus mansfieldi* Guensburg, 2012
- 850 *Apektocrinus ubaghsi* Guensburg and Sprinkle, 2009
- 851 *Athenacrinus broweri* Guensburg et al., 2020
- 852 *Carabocrinus treadwelli* Sinclair, 1945
- 853 *Eknomocrinus wahwahensis* Guensburg and Sprinkle, 2003
- 854 *Gaurocrinus nealli* (Hall, 1866)
- 855 *Glenocrinus globularis* Guensburg and Sprinkle, 2003
- 856 *Hybocrinus nitidus* Sinclair, 1945
- 857 *Proxenocrinus inyoensis* Strimple and McGinnis, 1972
- 858 *Titanocrinus sumralli* Guensburg and Sprinkle, 2003
- 859

860 **Table 3.** Matrix used in phylogenetic analysis. - = character state gap; ? = missing data.

861									
862	Taxon	Character Number							
863		1	11111	11111	22222	22222	33333	3333	
864		12345	67890	12345	67890	12345	67890	12345	6789
865	<hr/>								
866	<i>Stromatocystites pentangularis</i>	00000	0000-	00-0-	-0-0-	-----	-----	0-000	0---
867	<i>Kailidiscus chinensis</i>	000-0	0000-	10-0-	-0-0-	-----	-----	0-0?	0---
868	<i>Camptostroma rodgyi</i>	00000	00000	00-0-	---10	00---	-----	0-0-0	0---
869	" <i>Totiglobus</i> " <i>lloydi</i>	00000	0010-	10-0-	---0-	-----	-----	0-000	0---
870	<i>Pseudedriophus guensburgi</i>	00000	0010-	11-0-	-0-0-	-----	-----	2-00?	?---
871	<i>Kinzercystis durhami</i>	11111	-001-	00-0-	-0-0-	-----	-----	1-000	0---
872	<i>Lepidocystis wanneri</i>	11111	-001-	00-0-	-0-0-	-----	-----	1-00?	?---
873	<i>Gogia kitchnerensis</i>	11111	-001-	00-0-	-0-0-	-----	-----	2-10?	?---
874	<i>Rhopalocystis destombesi</i>	11111	-011-	04-00	-0-0-	-----	-----	3110?	?---
875	<i>Macrocystella mariae</i>	1111?	-011-	13--0	-0-0-	-----	-----	3110?	1---
876	<i>Hemicosmites pocillum</i>	1111?	-01?-	33--0	-0-0-	-----	-----	31101	1---
877	<i>Stephanocrinus gemmiformis</i>	1111?	-011-	15--0	-0-0-	-----	-----	31100	1---
878	<i>Eumorphocystis multiporata</i>	11111	-011-	23-00	-0-0-	-----	-----	31100	0---
879	<i>Ceratocystis perneri</i>	00--1	0000-	00---	-1010	10100	---00	0-00-	----
880	<i>Aethocrinus moorei</i>	00?00	10001	12001	11111	10000	01110	420?-	-000
881	<i>Alphacrinus mansfieldi</i>	00?00	10001	12011	0?112	11002	11101	4200-	-001
882	<i>Apektocrinus ubaghsi</i>	00000	10001	12000	11110	10000	-0010	4201-	-000
883	<i>Athenacrinus broweri</i>	00000	10001	12011	01112	11002	11101	4200-	-001
884	<i>Carabocrinus treadwelli</i>	00?-0	10001	12001	10111	10111	12110	4201-	-000
885	<i>Gaurocrinus nealli</i>	0-0?1	-1001	12101	11111	11100	10100	320?-	-111
886	<i>Hybocrinus nitidus</i>	00000	10001	10001	11110	11111	12110	42010	2000
887	<i>Eknomocrinus wahwahensi</i>	00??0	10001	12100	1?111	10000	00000	420?-	-000
888	<i>Proxenocrinus inyoensis</i>	00001	??001	12101	11111	11-00	10101	4?0?-	-111
889	<i>Glenocrinus globularis</i>	00??0	11000	1?100	1?111	10100	00000	420?-	-000
890	<i>Titanocrinus sumralli</i>	00?00	11000	02000	01111	10100	00000	4200-	-000
891	<hr/>								

892 **Figure Captions**

893

894

895 **Figure 1.** *Eumorphocystis multiporata* Branson and Peck, 1940, partial reconstruction, from

896 Parsley, 1982, included for orientation of subsequent images; by permission from The

897 Paleontological Institute, The University of Kansas, Lawrence.

898

899 **Figure 2.** *Eumorphocystis multiporata* Branson and Peck, 1940, 1279TX338 (NPL 93144), large900 partial theca with two adjacent pseudo-arm stubs, one longer, one shorter. **(1)** Coated oral view

901 showing long arm stub (left), pseudo-arm cover plates and brachial facet (just above and to right

902 and above scale), sharp keeled brachioles folded orally, one brachial nearly complete to tip,

903 proximal-most brachiolar short, wide, distal brachiolar with spinose processes and tiny biserial

904 cover plates, tapering to sharp termination, nearby thecal plates bearing dense diplopores; **(2)**905 Coated end-on view of pseudo-arm in **(1)**, broken at 7th floor plate beyond orals, tripartite

906 arrangement, backing plate below, small ambulacral groove and cover plates above, larger ovate

907 canal below; **(3)** Immersed short pseudo-arm stub and nearby theca, broken at distal margin of

908 ?third floor plate from oral, showing (from bottom to top), anchoring thecal plate with

909 diplopores, first backing plate, two sets of two blocky buttress plates forming a solid construct,

910 floor plates surrounding small dark pore (above), and brachial stubs (see Fig. 5.3); **(4)** lateral911 view of pseudo-arm stub in **(1)** with backing plates (below), buttress plates filling wedge at

912 thecal contact, large block-like, tumid, floor plates, and brachioles folded orally.

913

914 **Figure 3.** *Eumorphocystis multiporata* Branson and Peck, 1940, specimens showing pseudo-arm915 canal and adjacent morphology. **(1, 2)** OU 9049, **(1)** oral view of theca, plates partly obscured by

916 calcitic overgrowths, theca broken through C ambulacrum, arrow points to view of enlargement

917 in 2 (2); (2) magnified view showing exposed suture surface with normally concealed small
918 hemi-canal running down ambulacral mid-line ambulacral mid-line just above thecal interior
919 (arrow); (3, 5) TX1279.126, (3) oral view of well-preserved theca, thecal shoulder broken
920 through B ambulacrum (arrow) (5); (5) magnified view, AB oral showing long interrarial suture
921 at center-right with vertical "half diplopores", short suture, BC oral, on left showing hemi-canal,
922 concealed in articulated examples, along mid-line of B ambulacrum (arrow); (4) OU 238157,
923 deeply etched theca, E ray showing apparent small weathered pore (arrow); (6) 1107TX2, AB
924 interrarial view, face of pseudo-arm broken at fourth floor plate, small canal almost entirely within
925 floor plates.

926

927 **Figure 4.** *Eumorphocystis multiporata* Branson and Peck, 1940, showing pseudo-arms and stem
928 facet. (1-3), three specimens showing small canals near thecal juncture; (1) OU 9048, E ray,
929 canal small, assumed to be spar-filled, (2) OU 238159, small individual lacking buttress plates
930 (see Fig. 5.1), (3) 1404TX6 C ray, from intermediate-sized individual with large buttress plates
931 below and small wedge-shaped elements intercalating above, these are missing splinters,
932 otherwise plates are visible in crevasses (unseen in image) (see Fig. 5.2); (4) OU 238157 stem
933 facet with inset peg and groove crenularium.

934

935 **Figure 5.** Arm to calyx transition of early crinoids for comparison with *Eumorphocystis*
936 morphology. (1, 2) *Apektocrinus ubaghsi* Guensburg and Sprinkle, 2009, 1983TX1, D ray arm
937 trunk to calyx transition, (1) original image, (2) color overlay interpretation, color coding (used
938 in Fig. 5 as well) for specific body wall regions as follows: *Axial*— orange = floor plates, light
939 orange = brachioles (floor plate extensions), blue = lateral cover plates, purple = medial cover

940 plates; *perforate extraxial*— dark green = anchoring and backing plates, light green = buttress
 941 plate; *imperforate extraxial*— dark grey = brachials, light grey = laterals; (3) *Aethocrinus moorei*
 942 Ubaghs, 1969, uncertain orientation, lateral plate field collapsed indicating expanding arm
 943 coelomic cavity merging with main thecal cavity, floor and cover plates visible above, brachials
 944 below.

945
 946 **Figure 6.** Color-coded *Eumorphocystis multiporata* Branson and Peck, 1940, blastozoan feeding
 947 appendage constructs shown with restorations of early crinoid arms. (1-3) *E. multiporata*
 948 ontogenetic series (see Table 1), OU 238159, 1404TX6, and NPL 93144, respectively, pseudo-
 949 arms broken off at theca-arm juncture, the second floor plate distal to the orals, small circular
 950 canals within floor plates (for images, see Figs. 3.2, 3.3 and 1.3, respectively); (4) *E.*
 951 *multiporata*, pseudo-arm broken seven floor plates distal to the orals, large ovate canal; (5, 7)
 952 proximal arm cross sections of *Titanocrinus* and *Apektocrinus*, respectively; (6, 8, 9) Three
 953 blastozoan brachioles/arms with small canals, in cross section: rhipidocystid and *Gogia spiralis*
 954 Robinson, 1965, brachioles (from Sprinkle, 1973), and uniserial Cambrian blastozoan arm (from
 955 Clausen et al., 2009), respectively. Color coding: *axial*— orange = floor plates, light orange =
 956 brachioles (floor plate extensions), blue = lateral cover plates, purple = medial cover plates;
 957 *perforate extraxial*—dark green = radials and first backing plates, light green = buttress plates;
 958 *imperforate extraxial*— dark grey = brachials, light grey = laterals.

959
 960 **Figure 7.** Strict and 50% majority rule consensus trees for parsimony analysis of data matrix in
 961 Table 3. All node frequencies occur in 100% of trees except where indicated, and bootstrap

962 values are indicated by numbers in parentheses. See *Summary of character analysis findings*

963 below for definition of "pseudo-arm".

964

965