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1 **Taphonomy and ontogeny of early pelmatozoan echinoderms: a case**
2 **study of a mass-mortality assemblage of *Gogia* from the Cambrian of**
3 **North America**

4

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17

18 **ABSTRACT**

19

20 During the Palaeozoic, pelmatozoan echinoderms were substantially more diverse than
21 they are in modern oceans; however, the taphonomy and ontogeny of many of these
22 extinct groups is poorly known. Here, we report an exceptional mass-mortality
23 assemblage of the basal pelmatozoan *Gogia* sp., which consists of 106 articulated and
24 nearly complete specimens preserved on a single bedding plane. This slab was collected
25 from the middle Cambrian Spence Shale of Utah, USA, which is characterized by a

26 high-diversity echinoderm fauna that inhabited relatively deepwater distal-ramp settings
27 on a subsiding passive margin of Laurentia. The preferential orientation of specimens
28 strongly suggests that all the animals were entombed by a single unidirectional obrution
29 event; the specimens were most likely derived from a nearby area and represent a single
30 population that was living under the same environmental conditions. Statistical analysis
31 of the thecal heights of specimens, taken as a proxy for age, reveals a bimodal
32 distribution, suggesting that there were at least two episodes of larval settling in the
33 original population. This implies that gogiids displayed seasonal cycles of reproduction,
34 as do many modern echinoderms in equivalent environmental settings. During
35 ontogeny, the theca and stem of *Gogia* sp. grew by increasing the size of plates, as well
36 as through the incorporation of new plates (e.g., in the sutures between existing ones).
37 The brachioles, by contrast, were more conservative developmentally, and the size of
38 plates was maintained through ontogeny; they grew exclusively through the distal
39 addition of new plates. The epispires, which were used for respiration, are more
40 numerous in adults, as are the brachioles, indicating a degree of metabolic control on the
41 development of these structures. This study demonstrates that taxonomic studies of
42 gogiids should, wherever possible, consider a large number of specimens encompassing
43 a range of sizes in order to clearly distinguish between ontogenetic and interspecific
44 morphological variation.

45

46 *Keywords:* *Gogia*; echinoderms; Cambrian; population; taphonomy; ontogeny

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52 **1. Introduction**

53

54 Pelmatozoans are a major group of echinoderms, comprising all forms that developed
55 both a stem to elevate the theca above the seafloor and a fan of erect appendages for
56 filter feeding. Crinoids are the only living pelmatozoans; however, during the
57 Palaeozoic, numerous groups (e.g., blastoids, eocrinoids and rhombiferans –
58 collectively termed blastozoans) were important components of benthic marine
59 communities (Sprinkle, 1973; Foote, 1992; Nardin and Lefebvre, 2010). Because
60 blastozoans appear in the fossil record prior to crinoids (Guensburg and Sprinkle, 2001,
61 2007, 2009), they provide a unique opportunity to study the taphonomy and ontogeny of
62 the earliest pelmatozoans, with implications for the palaeobiology and early evolution
63 of the group. However, whereas studies of Palaeozoic crinoids are relatively common
64 (e.g., Brower, 1974, 2006; Meyer et al., 1989; Ausich and Sevastopulo, 1994; Webster,
65 1997; Gahn and Baumiller, 2004; Thomka et al., 2011; Ausich and Wood, 2012),
66 blastozoan taphonomy and ontogeny have received little attention to date. This is due, in
67 part, to the scarcity of abundant, well-preserved assemblages of fossil blastozoans with
68 articulated stems and feeding appendages.

69

70 Gogiids are the most abundant, diverse and widespread group of Cambrian stemmed
71 pelmatozoan echinoderms and have been reported from North and Central America,
72 Europe, North Africa and China (Sprinkle, 1973; Ubaghs, 1987; Parsley and Zhao,
73 2006; Nardin et al, 2009; Zamora et al., 2009). They belong to the Eocrinoidea, a
74 paraphyletic grade of basal blastozoans (Sprinkle, 1973; Smith, 1984; David et al.,
75 2000; Zamora et al., 2009), and are characterized by the possession of: 1) erect biserial

76 brachioles; 2) an irregular, polyplated theca with epispires for respiration; and 3) a
77 holdfast that is divided into a stem composed of numerous small plates and a distal
78 attachment structure. Well-preserved specimens demonstrate that gogiids attached to
79 microtopographic hard substrates (i.e., skeletal debris) in life, and typically inhabited
80 soft-bottom, quiet-water environments (Sprinkle, 1973; Lin et al., 2008a; Lin, 2009;
81 Zamora et al., 2009, 2010).

82
83 Abundant assemblages of gogiids are very rare (e.g., Balang and Kaili Faunas, China)
84 and tend to incorporate different specimens from the same bed or formation; such beds
85 are thought to be the product of multiple obrution events and, thus, do not provide
86 accurate data on the structure of a single population. Some authors have attempted to
87 reconstruct qualitative ontogenetic series from these populations (Parsley and Zhao,
88 2006; Zamora et al., 2009; Parsley, 2012), whereas others have examined the
89 taphonomy and palaeoecology of the assemblages (Lin et al., 2008b). However, because
90 these fossils are typically sourced and aggregated from a number of distinct populations,
91 these accumulations cannot be taken to represent single living communities and, hence,
92 do not preserve information on population structure or dynamics.

93
94 Here, we report a remarkable new mass-mortality assemblage of the gogiid *Gogia* sp.
95 from the middle Cambrian Spence Shale of western USA, which preserves 106
96 articulated individuals on a single bedding plane (Fig. 1, Supplementary Fig. 1,
97 Supplementary Video 1). All individuals are sourced from a single population and,
98 therefore, were likely exposed to the same environmental conditions during life; thus,
99 this assemblage represents a unique opportunity to analyse morphological plasticity and
100 ontogeny within a single population of gogiids. Moreover, because the specimens are

101 from the same obrution deposit, variations in taphonomic history are also minimized,
102 meaning that the preservational processes that led to the formation of this assemblage
103 can be fully elucidated.

104

105

106 **2. Material and methods**

107

108 The fossils are preserved on a single, large slab (approximately 63 mm in length; 31
109 mm in width on one side and 13 mm in width on the other) of grey-brown shale (Fig. 1,
110 Supplementary Fig. 1, Supplementary Video 1). The slab was originally collected by
111 Val and Glade Gunther from the Spence Shale Member of the Langston Formation,
112 Utah, USA, from a locality near Miner's Hollow, which is situated North of Brigham
113 City (Fig. 2). This corresponds to the basal middle Cambrian (provisionally called Stage
114 5 of Cambrian Series 3 in the most recent global chronostratigraphic framework;
115 Gradstein et al., 2012). The Spence Shale is a ~ 72 m thick sequence of interbedded
116 shales and limestones representing relatively deep marine, mixed carbonate-siliciclastic
117 slope deposition on the subsiding passive margin of Laurentia (Hintz and Robison,
118 1975; Rees, 1986; Robison, 1991; Liddell et al., 1997; Briggs et al., 2008). It contains
119 one of the highest diversity echinoderm faunas known from the middle Cambrian of
120 North America, including ctenocystoids, stylophorans and gogiids (Robison and
121 Sprinkle, 1969; Sprinkle, 1973, 1976; Sumrall and Sprinkle, 1999a; Sprinkle and
122 Collins, 2006). Around Miner's Hollow, localities range progressively upsection from
123 proximal ramp to more distal ramp and basinal settings (Liddell et al., 1997).
124 Echinoderm mass-mortality beds are common approximately 3 m from the top of the
125 Spence Shale Member (equivalent to unit MC6 of Liddell et al., 1997) but become

126 sparse near to the contact with the overlying High Creek Limestone Member (Val
127 Gunther, personal communication, 2012). The examined slab also contains some
128 complete specimens of the ctenocystoid *Ctenocystis utahensis*, fragments of trilobites
129 and carbonaceous algae (*Marpolia* sp.).

130

131 The gogiid specimens are preserved articulated and nearly complete as natural moulds;
132 all fossils were cast in latex and subsequently whitened with ammonium chloride
133 sublimate before photographs were taken. The orientations of specimens were measured
134 in order to elucidate the pattern of accumulation and distribution of individuals on the
135 slab (Figs. 1, 3A). Here, body axis was taken as the reference point for determining
136 specimen orientation, and this is defined as the line passing from the central part of the
137 thecal summit to the base. This has been used as a proxy for current direction in
138 previous studies (e.g., Lin et al., 2008b). The brachioles and the holdfast were not
139 considered when recording specimen orientations because, in many cases, they have
140 changes in direction (i.e., curved distal parts of the stem and brachioles) that are most
141 probably not the result of current orientation. Because the slab comes from a museum
142 collection and was not oriented in the field, we took an arbitrary position for north (0°)
143 in order to orientate our specimens (Fig. 1). A rose diagram of specimen orientations
144 and directional statistics were calculated using PAST (Hammer et al., 2001).

145

146 A number of different morphological measurements were made to enable ontogenetic
147 analysis of the gogiid assemblage. Thecal and stem heights of specimens were recorded
148 to provide estimates of how these structures developed. Moreover, we counted the
149 number of plate circlets to establish if the theca grew mainly through the addition of
150 new plates or fixed the number of plates in early ontogenetic stages and grew mainly by

151 increasing plate size – as is the case in some Palaeozoic groups of asteroids, crinoids,
152 blastoids and rhombiferans (Brower, 1974; Sumrall and Sprinkle, 1999b; Atwood and
153 Sumrall, 2012). To estimate the growth of the brachioles, we counted the number of
154 brachiolars per 2 mm in the proximal parts of the appendages. The number of brachioles
155 was also recorded for each individual to obtain an idea of the relationship between
156 thecal height and the number of brachioles.

157

158 We investigated correlations between measured morphological variables (allometry)
159 using both non-parametric tests (Spearman's rho and Kendall's tau) and ordinary least-
160 squares regression. In order to examine the age structure of the fossil community we
161 constructed size-frequency distributions, which are a frequently used tool in marine
162 biology, for investigating population structure in marine benthos. We restricted analyses
163 to thecal height (which is an accurate proxy for developmental stage in eocrinoids, see
164 Schlottko, 2007), stem length and the number of circlets/plates. We analysed the data in
165 R (R Development Core Team, 2010) using a model-based clustering method (Bayesian
166 Information Criterion, 'BIC') implemented in the package 'mclust' (Fraley and
167 Raftery, 2007).

168

169 The slab is currently housed in the Springer Collection of the Smithsonian National
170 Museum of Natural History (specimen number USNM 553409). In addition, a silicon
171 rubber cast has been deposited in the Natural History Museum, London under the
172 repository number EE 15372.

173

174

175 **3. Results**

176

177 *3.1. Morphological description*

178

179 *Gogia* sp. consists of three main morphological elements (Fig. 3B): the theca, the
180 brachioles and the holdfast. The theca ranges in height from 2.7 to 19.3 mm. Thecal
181 plates are polygonal and lack internal and external ornamentation; they are arranged in
182 between 5 and 11 circlets (Supplementary Table 1). Primary large thecal plates are
183 surrounded by multiple smaller secondary plates, as is the case in other gogiids and
184 several groups of early echinoderms (Sprinkle and Guensburg, 2001, fig. 3). Epispines
185 (sutural pores) are generally rare. In smaller specimens they occur exclusively near the
186 thecal summit, but in larger individuals they extend to the rest of the theca (Fig. 4). The
187 brachioles are long, slender, variable in number (ranging from 3 to 13) and non-
188 spiralled. They are composed of a biseries of brachiolar plates that alternate along an
189 abradial zig-zag suture (Figs. 3, 4). Cover plates are mounted on brachiolars in a ratio of
190 2:1. The transition from the theca to the holdfast is gradual in most specimens, and there
191 is no clear difference in plating between the basal part of the theca and the proximal part
192 of the stem (Fig. 5). The stem ranges from 1.6 to 16.6 mm in length and consists of a
193 hollow tube composed of small, globular plates. The diameter decreases toward the
194 distal end, which terminates in an expanded attachment structure (Fig. 3B). A complete
195 formal description of this new species of *Gogia* is currently being prepared by James
196 Sprinkle and Bryan Wilbur and is thus not provided in this manuscript.

197

198 *3.2. Articulation patterns*

199

200 In almost all of the specimens on the slab, the theca is preserved articulated and with no
201 evidence of significant skeletal disruption, apart from thecal collapse/flattening caused
202 by the decay of soft tissues/burial. The stems are also articulated in most individuals,
203 but in some cases the distal parts are strongly curved or bent (Fig. 5). The brachioles
204 are, for the most part, fully articulated with the cover plates mounted on the brachiolaria,
205 but in a few cases there is some disarticulation of the distal elements. There are no
206 disarticulated plates from gogiids or other echinoderms in the same bedding plane. Lin
207 et al. (2008b) were the first to analyse the taphonomy of gogiids, and they divided
208 specimens into three categories depending on their degree of disarticulation. Our
209 specimens belong to group 1, which consists of all gogiids with a fully articulated theca
210 and holdfast and relatively complete brachioles.

211

212 *3.3. Distribution and entombment patterns*

213

214 Specimen orientations were determined for 74 individuals of *Gogia* sp. on the slab. It
215 was not possible to accurately determine the orientations of the remaining 32
216 individuals due to incomplete preservation of the theca. A rose diagram showing the
217 orientation of the specimens is shown in Fig. 1; this indicates that individuals were
218 preferentially oriented to the west, at approximately 258°.

219

220 Lin et al. (2008b) described five entombment patterns in gogiids from the Cambrian of
221 China. The majority of our specimens conform to entombment pattern type 2, meaning
222 that they are oriented parallel to one another with brachioles splayed out in a fan-shaped
223 pattern (Fig. 3C). However, other entombment patterns occur in a few specimens (Fig.
224 3D, E, Supplementary Fig. 1, Supplementary Video 1).

225

226 *3.4. Population structure*

227

228 The full results of non-parametric correlation tests are given in Fig. 6 and are
229 summarized here; thecal height and stem length have a strong positive (and statistically
230 significant) correlation (Spearman's $\rho = 0.79$, $p < 0.001$). Weaker (although still
231 significant) correlations exist between thecal height and the minimum number of
232 brachioles (Spearman's $\rho = 0.54$, $p < 0.001$) and between stem length and the number
233 of circlets/plates (Spearman's $\rho = 0.45$, $p < 0.05$). The number of brachiolaris every 2
234 mm in the proximal parts of the brachioles is not correlated with any of the other
235 measured morphological traits. Ordinary least-squares regression analysis shows a
236 strong linear dependence between log-transformed thecal height and stem length ($R^2 =$
237 0.78 ; see Fig. 7).

238

239 The size-frequency distribution of thecal heights is considerably right-skewed and
240 bimodal, with one pronounced peak at 8–9 mm and one smaller peak in the range 15–20
241 mm (Fig. 8). These observations are supported by the results of BIC, which resolves a
242 clear peak at two groups with equal variance (Table 1, Fig. 8); these two groups are
243 identified with mean thecal heights at 8.8 and 15.9 mm. BIC also resolves two groups
244 with equal variance in the number of circlets/plates but only one group based on the
245 stem length data (Table 1).

246

247 **4. Discussion**

248

249 *4.1. Post-mortem depositional history*

250

251 The multi-element skeleton of gogiids is a good indicator of the duration and nature of
252 post-mortem depositional processes, similar to other pelmatozoan echinoderms (Brett
253 and Baird, 1986; Meyer et al., 1990; Brett et al., 1997). Superficially, gogiids resemble
254 crinoids in their body organization, but there are also clear differences in the
255 construction of their component parts. In gogiids, thecal plates were loosely articulated,
256 probably with connective tissue, whereas in many groups of crinoids and more derived
257 blastozoans the plates were rigidly fused. Furthermore, in almost all crinoids the stem is
258 composed of single piece (holomeric) columnals, which were tightly fused together by
259 mutable collagenous tissue in life (Hess et al., 1999); in contrast, the stem of gogiids is a
260 polyplated hollow tube consisting of small and loosely articulated elements. Brachioles
261 are constructed rather differently to crinoid arms (Sprinkle, 1973; David et al., 2000;
262 Guensburg and Sprinkle, 2007, 2009), being delicate structures that are more
263 comparable to pinnules than to the main part of a crinoid arm. Crinoid brachial
264 articulations also had ligaments or muscles, whereas only simple ligamentary pits occur
265 in gogiids. Ligaments are generally more robust to decay than are muscles (Ausich and
266 Baumiller, 1993), however, gogiid brachiolar articulations have a smaller surface area
267 than most crinoid arms, and therefore may have been susceptible to rapid
268 disarticulation. As a result, gogiids were likely more prone to post-mortem
269 disarticulation than crinoids, and the impact of taphonomic processes probably differed
270 between these two groups.

271

272 Crinoids preserving articulated arms and columnals are considered to indicate rapid
273 burial with minimal transport history (i.e. close to life position, see Meyer et al., 1990),
274 with the exception of crinoids with tightly-sutured plates (see Brett and Baird, 1986).

275 Considering the exceptional state of preservation of our specimens and the special
276 properties of the gogiid skeleton – which would have disarticulated readily after death
277 (see also Liddell et al., 1997) – we infer that the specimens of *Gogia* sp. described
278 herein were buried rapidly and that they represent a life assemblage that was originally
279 preserved in-place (autochthonous) or underwent minimal transport from nearby
280 (parautochthonous). The exceptional preservation of articulated hexactinellid sponges
281 from elsewhere in this sequence indicates that instances of event burial were relatively
282 widespread in this depositional setting (Rigby, 1980; Gunther and Gunther, 1981).
283 Additional support for this taphonomic mode is offered by the preferential orientation of
284 specimens (at approximately 258°) and the entombment pattern (predominantly type 2
285 under the scheme of Lin et al., 2008b), which are suggestive of no or limited transport,
286 with individuals aligned by a unidirectional current and rapidly buried in feeding
287 position by a single event of sedimentation. Last, our statistical analyses recover two
288 distinct size modes in the thecal heights of specimens; bimodal size distributions are
289 rarely recovered in palaeontological datasets and usually indicate instances of
290 catastrophic burial that preserve the original ecological signature of age cohorts
291 (Sheldon, 1965; Cummins et al., 1986). Therefore, we interpret the polymodality of our
292 size-frequency data as representing the original population structure of the assemblage,
293 rather than the result of post-mortem transport and size sorting.

294

295 *4.2. Atypical stem morphologies*

296

297 Several specimens of *Gogia* sp. exhibit unusually curved or bent distal stems (Fig. 5),
298 but the cause of this posture is unclear. In nearly all cases, sessile stemmed echinoderms
299 are thought to have attached at an early ontogenetic stage and subsequently spent their

300 entire life in the same place. There are a few exceptions in recent stalked crinoids, some
301 of which are capable of moving using their feeding appendages (Baumiller and
302 Messing, 2007), but this was clearly not the case in gogiids because they lacked
303 musculature in their brachioles (and stem). Based on the presence of a distal attachment
304 structure in the studied specimens and observations of other gogiid species (Sprinkle,
305 1973; Lin et al., 2008a; Lin, 2009; Zamora et al., 2009), we suggest that *Gogia* sp. was
306 permanently attached to a hard substrate in life. Thus, the atypical stem morphologies
307 are almost certainly not modifications related to locomotion or anchoring.

308

309 Curved/bent distal stems occur in only a relatively small number of individuals, and this
310 argues against the posture being due to the post-mortem decay of soft tissues (e.g.,
311 causing contortion of the stem) because such a mechanism would be expected to operate
312 equally in all specimens (which are otherwise almost identically preserved). A more
313 probable explanation is that the posture relates to the high velocity and turbulence of the
314 flow that buried the specimens, disturbing their life position.

315

316 *4.3. Bimodal population structure*

317

318 Based on the preservation, orientation and entombment patterns of *Gogia* sp., it seems
319 almost certain that all the individuals on the slab originally came from the same
320 population/area and, thus, were exposed to the same environmental conditions during
321 life (see section 4.1.). The studied community is dominated by small- to intermediate-
322 sized individuals, with relatively few larger individuals. Statistically, based on thecal
323 heights, the size-frequency data are best described as a mixture of two distributions.
324 This is in close agreement with similar analyses of the number of circlets/plates but in

325 disagreement with the stem length data – despite the strong correlation between thecal
326 height and stem length (as revealed by non-parametric tests and least-squares
327 regression), which would suggest that stem length increased throughout the lifespan of
328 individuals. This disagreement can potentially be explained due to taphonomic bias –
329 only a relatively small number of individuals have attachment disc structures preserved
330 (some may have been buried slightly deeper and, therefore, could be concealed beneath
331 the surface of the slab, or otherwise might have been torn off during
332 burial/transportation), suggesting that many of the measured stem lengths are
333 incomplete. Any analyses pertaining to stem lengths are preliminary and, therefore,
334 should be viewed with caution. These analyses do suggest, however, that both thecal
335 height and the number of circlets/plates are potentially good proxies for age in gogiid
336 echinoderms.

337

338 Organisms with seasonal reproduction and recruitment typically have distinct modes in
339 size-frequency distributions, which correspond to individual age classes (e.g., Billett
340 and Hansen, 1982; Fujita and Ohta, 1990). Modern echinoderm meadow-type
341 communities, such as those consisting of holothurians (Rowe, 1971, 1972; Billett and
342 Hansen, 1982), ophiuroids (Fujita and Ohta, 1989, 1990; Packer et al., 1994) and
343 echinoids (Forcucci, 1994), have been studied in this context in order to make
344 inferences about ecology, environmental stability and age structure.

345

346 In terms of interpreting the population structure and dynamics of fossil echinoderm
347 accumulations, studies on modern communities provide an analytical framework;
348 accumulations of small individuals with extremely similar sizes (for example, in
349 holothurians – see Rowe, 1971, 1972; Billett and Hansen, 1982) are typically

350 interpreted as representing a single highly synchronous reproductive event and, in
351 general, a sedimentary environment characterized by turbidity flows and mass burials
352 (Billet and Hansen, 1982). In contrast, two or more modes (see size-frequency analyses
353 by Fujita and Ohta, 1990 on populations of the ophiuroid *Ophiura sarsa*) indicate a
354 mixture of age classes. Packer et al. (1994) obtained similar results for populations of *O.*
355 *sarsa* from Maine, USA, finding a distinctly bimodal distribution with a sharp peak in
356 the frequencies of small individuals interpreted as representing a single cohort. A
357 second, broader peak in larger individuals was interpreted as representing the
358 accumulation of several older cohorts. The *Gogia* sp. meadow-type community reported
359 herein is similar to those described by Fujita and Ohta (1990) and Packer et al. (1994);
360 the population is made up of multiple size modes that likely represent several discrete
361 age classes. This in turn suggests that the immediate palaeoenvironment was relatively
362 stable, with long periods of relative quiescence (long enough to allow multiple episodes
363 of spawning and recruitment) between catastrophic obrution and mass-burial events. In
364 terms of fossil material, similar patterns have been documented in the edrioasteroid
365 *Curviriordo stecki* and were explained as the result of a hiatus in recruitment (e.g.,
366 seasonal breeding) or some other factor that greatly restricted recruitment of new larvae
367 for a period (Sumrall, 2010; Shroat-Lewis et al., 2011).

368

369 The age structure of the studied population also allows broader inferences to be made
370 regarding the reproductive biology of gogiid echinoderms. The identification of
371 multiple age classes implies that the production and release of gametes was likely
372 seasonal, leading to pulses of recruitment and settlement that were subsequently
373 reflected in size modes. In modern continental shelf (deeper than ~ 500 m) and deep-sea
374 communities, coordinated reproduction is triggered by a seasonal flux of organic matter

375 and phytodetritus from surface waters (e.g., Tyler and Young, 1992; Morales-Nin and
376 Panfili, 2005). Therefore, these data provide evidence to suggest that this flux was
377 already well-established and a significant control on organismal biology and ecology by
378 the middle Cambrian – a comparatively short time after the explosive increase in both
379 the volume and character of planktonic diversity at the base of the Phanerozoic (see
380 Butterfield, 2009, 2011).

381

382 *4.4. Ontogeny*

383

384 Previous studies of gogiid ontogeny based on Chinese material identified several
385 different developmental stages defined by thecal heights and certain morphological
386 characters (Parsley and Zhao, 2006; Parsley, 2012), and these can be contrasted with our
387 abundant material of *Gogia* sp. Parsley and Zhao (2006) recognized juvenile, advanced
388 juvenile, mature and advanced mature or gerontic stages in *Sinoeocrinus lui*, and this
389 classification was later revised based on additional genera to give a total of three stages
390 (juvenile, mature and gerontic) and seven substages (Parsley, 2012). Parsley (2012) also
391 identified five characters that might change with ontogeny in gogiids: (1) the number
392 and morphology of the brachioles; (2) the number and arrangement of the thecal plates;
393 (3) the number, morphology and position of epispines; (4) the size of the stem; and (5)
394 the morphology of the distal attachment structure.

395

396 The specimens of *Gogia* sp. that we describe range from 2.7 to 19.3 mm in size (Fig. 4,
397 Supplementary Table 1). This size interval encompasses all the stages that Parsley and
398 Zhao (2006) and Parsley (2012) defined for *Sinoeocrinus lui*, *Globoeocrinus globulus*
399 and *Guizhoueocrinus yui*. A histogram of thecal height measurements indicates that

400 *Gogia* sp. grows isometrically, and there are no statistically supported differences
401 between any of the size groupings previously proposed by Parsley and Zhao (2006) and
402 Parsley (2012). Therefore, although thecal height remains a justifiable proxy for age,
403 gogiid post-metamorphic development was most likely a continuous process, and it
404 seems unwise to assign specimens to distinct ontogenetic stages (as opposed to
405 allocating them to a discrete age cohort within a larger population) on the basis of thecal
406 height alone.

407

408 Several characters are positively correlated with thecal height, suggesting that they also
409 changed during ontogeny. Stem length has the most significant correlation (Spearman's
410 $\rho = 0.79$, $p < 0.001$; Kendall's $\tau = 0.64$, $p < 0.001$), implying that gogiids increased
411 the length of the stem in concert with the size of their theca, although the mechanisms
412 underlying the growth of these distinct elements may have been rather different.

413 Comparing the stems of specimens belonging to different ontogenetic stages (e.g. Fig.
414 5A vs. 5E), it appears that they grew chiefly by incorporating new plates, but the
415 accretion of calcite on existing ossicles probably also played a role, with the stem plates
416 up to four times larger in the larger gogiid individuals. However, the incomplete
417 preservation of stems in a number of the specimens (see section 4.3.) implies that many
418 of our measures of stem length are underestimates, and the stem may actually have
419 grown at a faster rate than currently documented. An additional character that has a
420 positive correlation with thecal height (albeit a weaker one), is the number of thecal
421 plate circlets, which ranges from 5 to 11 (Spearman's $\rho = 0.37$, $p < 0.01$; Kendall's
422 $\tau = 0.29$, $p < 0.01$). This may have been one further mechanism by which gogiids
423 were able to increase the size of their theca during development.

424

425 The size and number of thecal plates are additional characters that were modified during
426 ontogeny. Observations of plate junctures show that smaller individuals are primarily
427 composed of a low number of relatively large plates, which are termed primary thecal
428 plates (Fig. 4). In larger, older individuals, secondary thecal plates were added between
429 these junctures (Fig. 9), and there was also a considerable increase in the relative size of
430 these newly added plates with development (Fig. 9).

431

432 Epispire are another feature that changed markedly in development; this has previously
433 been documented in Cambrian edrioasteroids (Zamora et al., in press) and gogiids
434 (Parsley, 2012). In the smaller specimens of *Gogia* sp. with a mean thecal height of 4
435 mm, epispire appear close to the summit. In the larger specimens, epispire tend to
436 occur also in the upper part of the theca. In very large specimens with a mean thecal
437 height of 15–20 mm, epispire are typically present throughout the upper three-quarters
438 of the theca (Figs. 4, 9). Thus, there is apparently some relationship between increasing
439 thecal height and the widespread emplacement of epispire. However, it is important to
440 note this is not a universal pattern in *Gogia* sp., and some larger individuals exhibit less
441 extensive development of epispire than expected (compare Fig. 4M and Fig. 4N). In
442 such cases, heterochronic processes may have brought about changes in the timing of
443 epispire development.

444

445 Parsley and Zhao (2006) showed that the number of brachioles increased during gogiid
446 ontogeny, and this fits with our findings for *Gogia* sp.; the number of brachioles is
447 positively correlated with thecal height (Spearman's $\rho = 0.54$, $p < 0.001$; Kendall's
448 $\tau = 0.42$, $p < 0.001$). A model for ambulacral development based on edrioasteroids
449 suggests that the first ambulacra to form were the lateral branches BC and DE, followed

450 by A, and ending with the branching of the lateral branches into separate B, C, D and E
451 (Sumrall and Wray, 2007). Similar patterns have been observed in gogiids, resulting in
452 the formation of five ambulacra and five brachioles (Parsley and Zhao, 2006). It has
453 been suggested that the increase in the number of brachioles after the acquisition of
454 five-fold symmetry was triggered by a change from simple ambulacra to heterotomous
455 ambulacra, together with a subsequent increase in the number of facets for the
456 attachment of brachioles located at the end of each ambulacral branch. This model
457 provides a clear picture of when during ontogeny the number and size of brachioles
458 increased but does not inform on whether brachioles grew through the addition of new
459 plates or by increasing the size of existing ones. There is no significant correlation
460 between thecal height and the number of brachiolar per two millimetres in the proximal
461 part of the brachioles, demonstrating that these plates did not increase in size during
462 ontogeny. Therefore, the increased size of brachioles in adult gogiids is most probably
463 the product of adding new plates in their distal parts.

464

465 To sum up, different mechanisms controlled development in different parts of the gogiid
466 skeleton. The theca grew through the addition of new plates but also by accretion of
467 calcite on existing plates. The stem grew through a similar mechanism to the theca,
468 chiefly by adding new plates, but also through increasing the size of the existing
469 ossicles. Whether the new elements were added at the stem–theca contact, or
470 intercalated along the stem length, is not something we can unambiguously address
471 based on our material; however, the presence of primary stem plates bounded by small
472 secondary elements in larger specimens points to the later mechanism as the most
473 plausible. The brachioles grew through the addition of new plates in their distal parts,

474 and there is no evidence that additional plates were inserted along their length, or that
475 plate sizes increased with ontogeny.

476

477 *4.5. Taxonomic recommendations*

478

479 The ontogenetic sequence of gogiids elucidated in section 4.4. demonstrates that
480 complete developmental staging series are crucial if we are to accurately define species
481 in the fossil record. The shape of the theca and the spiralled condition of the brachioles
482 do not change during the ontogeny of a given species, but certain other features can vary
483 dramatically in development. These include the number and position of epispires, which
484 first appeared close to the thecal summit before extending over the entire theca; the
485 length of the theca and the stem, both of which increased during ontogeny; and the
486 number of brachioles, which is greatest in adult specimens.

487

488 It is also possible that certain gogiid species developed features earlier in ontogeny than
489 others. For example, thecal plates in small specimens of *Gogia hobbsi* (mean thecal
490 heights of 4–11 mm; Sprinkle, 1973) have characteristics restricted to adults in other
491 gogiid species, such as the abundant and well-developed epispires of adult specimens of
492 *Sinoeocrinus lui* (Parsley and Zhao, 2006). Moreover, specimens of *Gogia gondi*
493 described by Ubaghs (1987) have well-developed epispires all over the theca in
494 individuals with thecal heights of 5 mm. By contrast, specimens that are similar in size
495 to *Gogia* sp. either lack epispires entirely or rarely have them in only the upper part of
496 the theca.

497

498 These examples clearly indicate that the evolution of gogiids was in part controlled by
499 heterochronic processes. Future work should focus on establishing complete
500 ontogenetic series for multiple gogiid taxa and subsequently carrying out a cladistic
501 analysis of the group in order to identify these aspects of their palaeobiology. Several
502 characters that have traditionally been used to define species have been shown herein to
503 change ontogenetically; and, therefore, we should be cautious when erecting new
504 species based on differences in these features. Sprinkle (1973) provided the most
505 comprehensive study of gogiids from North America to date, and summarized in a table
506 (Sprinkle, 1973, table 2) the different features that could be used to differentiate species.
507 Our work plus previous studies of gogiid ontogeny (Parsley and Zhao, 2006; Zamora et
508 al., 2009; Parsley, 2012) clearly show that several of these features vary ontogenetically,
509 casting serious doubts on their validity for taxonomy. This study highlights the
510 importance of using large numbers of specimens when carrying out work on
511 echinoderm systematics.

512

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514

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527

528

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707

708 **Figure and table captions**

709

710 **Fig. 1.** Schematic drawing of the studied slab preserving a mass assemblage of *Gogia*
711 sp. A rose diagram shows the preferred orientation of specimens (the position of North,
712 0°, is arbitrary) and the results of directionality tests are given in the bottom left corner.

713

714 **Fig. 2.** Regional map of northeastern Utah, USA, showing the locality from which the
715 slab was collected (starred). Base map redrawn from Liddell et al. (1997). Lined area in
716 bottom right of map corresponds to the eastern limit of the Spence Shale.

717

718 **Fig. 3.** General morphology of *Gogia* sp. A. Seven complete specimens showing a
719 range of orientations; arrows indicate the reference points for determining specimen

720 orientations, which were used to build the rose diagram in Fig. 1. B. Complete specimen
721 showing the diagnostic characters of eocrinoids. Abbreviations: brs, brachioles; th,
722 theca; st, stem; hd, holdfast. C–E. A number of specimens showing a range of sizes and
723 orientations. All photographs are from latex casts whitened with NH₄Cl sublimate.

724

725 **Fig. 4.** Growth series of *Gogia* sp. A. Smallest specimen with a thecal height of 0.27
726 cm, very few brachioles and a wide and short stem. B. Specimen with a thecal height of
727 0.39 cm and a longer and thinner stem. Theca composed of only primary thecal plates.
728 C. Specimen with a thecal height of 0.53 cm, showing multiple brachioles and with
729 secondary thecal plates starting to appear between plate junctures. D. Specimen with a
730 thecal height of 0.58 cm in which the first small epispires start to appear close to the
731 thecal summit. E. Specimen with a thecal height of 0.83 cm. F. Specimen with a thecal
732 height of 0.81 cm. G. Specimen with a thecal height of 0.87 cm, showing the generation
733 of new thecal plates on the left side. H. Specimen with a thecal height of 0.93 cm. I.
734 Specimen with a thecal height of 0.93 cm in which epispires start to appear in the upper
735 portion of the theca. J. Two specimens with thecal heights of 0.82 and 0.99 cm. K.
736 Specimen with a thecal height of 0.93 cm in which very small epispires start to appear
737 in the middle part of the theca. L. Relatively large specimen with a thecal height of 1.4
738 cm in which epispires are absent in the middle part of the theca, even though they are
739 present in other specimens with a similar size. M. Large specimen with a thecal height
740 of 1.72 cm and an atypical distal end of the stem. N. Large specimen with a thecal
741 height of 1.73 cm and with epispires present in the upper three-quarters of the theca and
742 with abundant brachioles. All photographs are from latex casts whitened with NH₄Cl
743 sublimate.

744

745 **Fig. 5.** Morphological variation in the stem of *Gogia* sp. A. Very short stem of an early
746 juvenile with a thecal height of 0.27 cm. B. Two stems with distal curved parts. C. Stem
747 from a relatively large specimen showing S-shaped curvature. D. Strongly bent stem. E.
748 Normal stem with a distal attachment structure; compare with the stem of an early
749 juvenile in A. F. Stem with a distal loop. All photographs are from latex casts whitened
750 with NH₄Cl sublimate.

751

752 **Fig. 6.** Scatterplot matrix of all studied morphological traits showing the results of non-
753 parametric correlation tests. Panels in the bottom left are scatterplots with lowess
754 regression lines (dashed, black); correlations and significance levels are given in the
755 corresponding panels in the upper right (Spearman's rho values in black, Kendall's tau
756 values in grey). Abbreviations: ***, $p < 0.001$; **, $p < 0.01$; *, $p < 0.05$; ·, $p < 0.1$.

757

758 **Fig. 7.** Upper panel: raw scatterplot of thecal height vs. stem length in the measured
759 specimens ($n = 38$). Lower panel: logged data with ordinary least-squares regression
760 line ('OLS', black), 95% confidence intervals (light grey) and 95% prediction intervals
761 (dark grey).

762

763 **Fig. 8.** Upper panels show BIC plots for thecal height (A), number of circlets/plates (B)
764 and stem length (C), produced using the package *mclust* in R (Fraley and Rafferty,
765 2007). Peaks in BIC plots indicate the most likely number of components/groups; note
766 that both thecal height and number of circlets/plates show peaks at two groups. Lower
767 panels (D–F) show corresponding size-frequency distributions for measured traits;
768 density functions from BIC analyses have been superimposed in black to illustrate the
769 distribution of groups.

770

771 **Fig. 9.** Details of the theca for three different ontogenetic stages in *Gogia* sp. A.
772 Specimen with a thecal height of 0.39 cm showing few plate circlets, large primary
773 thecal plates and very small epispires in only the uppermost part of the theca. B.
774 Specimen with a thecal height of 0.81 cm showing more thecal plates than in the
775 previous stage and with new plates appearing in plate junctures; epispires occur in the
776 upper part of the theca, close to the summit. C. Specimen with a thecal height of 1.73
777 cm and a theca composed of mostly large thecal plates and with epispires present in the
778 upper three-quarters of the theca. All photographs are from latex casts whitened with
779 NH₄Cl sublimate.

780

781 **Table 1.** Summary table with parameters and results of BIC analyses.

782

783

784 **Appendix A. Supplementary data**

785

786 **Supplementary Fig. 1.** Photograph of the studied slab (USNM 553409) with numbered

787 specimens of *Gogia* sp.

788

789 **Supplementary Video 1.** Video showing the studied slab and latex casts of different

790 specimens of *Gogia* sp.

791

792 **Supplementary Table 1.** Measurements and morphological data for specimens of

793 *Gogia* sp. For individual specimen numbers, see Supplementary Fig. 1.