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

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ABSTRACT

During the Palaeozoic, pelmatozoan echinoderms were substantially more diverse than they are in modern oceans; however, the taphonomy and ontogeny of many of these extinct groups is poorly known. Here, we report an exceptional mass-mortality assemblage of the basal pelmatozoan *Gogia* sp., which consists of 106 articulated and nearly complete specimens preserved on a single bedding plane. This slab was collected from the middle Cambrian Spence Shale of Utah, USA, which is characterized by a high-diversity echinoderm fauna that inhabited relatively deepwater distal-ramp settings on a subsiding passive margin of Laurentia. The preferential orientation of specimens strongly suggests that all the animals were entombed by a single unidirectional obrution event; the specimens were most likely derived from a nearby area and represent a single population that was living under the same environmental conditions. Statistical analysis of the thecal heights of specimens, taken as a proxy for age, reveals a bimodal distribution, suggesting that there were at least two episodes of larval settling in the original population. This implies that gogiids displayed seasonal cycles of reproduction, as do many modern echinoderms in equivalent environmental settings. During ontogeny, the theca and stem of *Gogia* sp. grew by increasing the size of plates, as well as through the incorporation of new plates (e.g., in the sutures between existing ones). The brachioles, by contrast, were more conservative developmentally, and the size of plates was maintained through ontogeny; they grew exclusively through the distal addition of new plates. The epispires, which were used for respiration, are more numerous in adults, as are the brachioles, indicating a degree of metabolic control on the development of these structures. This study demonstrates that taxonomic studies of gogiids should, wherever possible, consider a large number of specimens encompassing a range of sizes in order to clearly distinguish between ontogenetic and interspecific morphological variation.

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

1. Introduction

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

Gogiids are the most abundant, diverse and widespread group of Cambrian stemmed pelmatozoan echinoderms and have been reported from North and Central America, Europe, North Africa and China (Sprinkle, 1973; Ubaghs, 1987; Parsley and Zhao, 2006; Nardin et al, 2009; Zamora et al., 2009). They belong to the Eocrinoidea, a paraphyletic grade of basal blastozoans (Sprinkle, 1973; Smith, 1984; David et al., 2000; Zamora et al., 2009), and are characterized by the possession of: 1) erect biserial brachioles; 2) an irregular, polyplated theca with epispires for respiration; and 3) a holdfast that is divided into a stem composed of numerous small plates and a distal attachment structure. Well-preserved specimens demonstrate that gogiids attached to microtopographic hard substrates (i.e., skeletal debris) in life, and typically inhabited soft-bottom, quiet-water environments (Sprinkle, 1973; Lin et al., 2008a; Lin, 2009; Zamora et al., 2009, 2010).

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

Here, we report a remarkable new mass-mortality assemblage of the gogiid *Gogia* sp. from the middle Cambrian Spence Shale of western USA, which preserves 106 articulated individuals on a single bedding plane (Fig. 1, Supplementary Fig. 1, Supplementary Video 1). All individuals are sourced from a single population and, therefore, were likely exposed to the same environmental conditions during life; thus, this assemblage represents a unique opportunity to analyse morphological plasticity and ontogeny within a single population of gogiids. Moreover, because the specimens are from the same obrution deposit, variations in taphonomic history are also minimized, meaning that the preservational processes that led to the formation of this assemblage can be fully elucidated.

2. Material and methods

The fossils are preserved on a single, large slab (approximately 63 mm in length; 31 mm in width on one side and 13 mm in width on the other) of grey-brown shale (Fig. 1, Supplementary Fig. 1, Supplementary Video 1). The slab was originally collected by Val and Glade Gunther from the Spence Shale Member of the Langston Formation, Utah, USA, from a locality near Miner’s Hollow, which is situated North of Brigham City (Fig. 2). This corresponds to the basal middle Cambrian (provisionally called Stage 5 of Cambrian Series 3 in the most recent global chronostratigraphic framework; Gradstein et al., 2012). The Spence Shale is a ~ 72 m thick sequence of interbedded shales and limestones representing relatively deep marine, mixed carbonate-siliciclastic slope deposition on the subsiding passive margin of Laurentia (Hintz and Robison, 1975; Rees, 1986; Robison, 1991; Liddell et al., 1997; Briggs et al., 2008). It contains one of the highest diversity echinoderm faunas known from the middle Cambrian of North America, including ctenocystoids, stylophorans and gogiids (Robison and Sprinkle, 1969; Sprinkle, 1973, 1976; Sumrall and Sprinkle, 1999a; Sprinkle and Collins, 2006). Around Miner’s Hollow, localities range progressively upsection from proximal ramp to more distal ramp and basinal settings (Liddell et al., 1997). Echinoderm mass-mortality beds are common approximately 3 m from the top of the Spence Shale Member (equivalent to unit MC6 of Liddell et al., 1997) but become sparse near to the contact with the overlying High Creek Limestone Member (Val Gunther, personal communication, 2012). The examined slab also contains some complete specimens of the ctenocystoid *Ctenocystis utahensis*, fragments of trilobites and carbonaceous algae (*Marpolia* sp.).

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

A number of different morphological measurements were made to enable ontogenetic analysis of the gogiid assemblage. Thecal and stem heights of specimens were recorded to provide estimates of how these structures developed. Moreover, we counted the number of plate circlets to establish if the theca grew mainly through the addition of new plates or fixed the number of plates in early ontogenetic stages and grew mainly by increasing plate size – as is the case in some Palaeozoic groups of asteroids, crinoids, blastoids and rhombiferans (Brower, 1974; Sumrall and Sprinkle, 1999b; Atwood and Sumrall, 2012). To estimate the growth of the brachioles, we counted the number of brachiolars per 2 mm in the proximal parts of the appendages. The number of brachioles was also recorded for each individual to obtain an idea of the relationship between thecal height and the number of brachioles.

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

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

3. Results

3.1. Morphological description

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

3.2. Articulation patterns

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

3.3. Distribution and entombment patterns

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

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

3.4. Population structure

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

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

4. Discussion

4.1. Post-mortem depositional history

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

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

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

4.2. Atypical stem morphologies

Several specimens of *Gogia* sp. exhibit unusually curved or bent distal stems (Fig. 5), but the cause of this posture is unclear. In nearly all cases, sessile stemmed echinoderms are thought to have attached at an early ontogenetic stage and subsequently spent their entire life in the same place. There are a few exceptions in recent stalked crinoids, some of which are capable of moving using their feeding appendages (Baumiller and Messing, 2007), but this was clearly not the case in gogiids because they lacked musculature in their brachioles (and stem). Based on the presence of a distal attachment structure in the studied specimens and observations of other gogiid species (Sprinkle, 1973; Lin et al., 2008a; Lin, 2009; Zamora et al., 2009), we suggest that *Gogia* sp. was permanently attached to a hard substrate in life. Thus, the atypical stem morphologies are almost certainly not modifications related to locomotion or anchoring.

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

4.3. Bimodal population structure

Based on the preservation, orientation and entombment patterns of *Gogia* sp., it seems almost certain that all the individuals on the slab originally came from the same population/area and, thus, were exposed to the same environmental conditions during life (see section *4.1.*). The studied community is dominated by small- to intermediate-sized individuals, with relatively few larger individuals. Statistically, based on thecal heights, the size-frequency data are best described as a mixture of two distributions. This is in close agreement with similar analyses of the number of circlets/plates but in disagreement with the stem length data – despite the strong correlation between thecal height and stem length (as revealed by non-parametric tests and least-squares regression), which would suggest that stem length increased throughout the lifespan of individuals. This disagreement can potentially be explained due to taphonomic bias – only a relatively small number of individuals have attachment disc structures preserved (some may have been buried slightly deeper and, therefore, could be concealed beneath the surface of the slab, or otherwise might have been torn off during burial/transportation), suggesting that many of the measured stem lengths are incomplete. Any analyses pertaining to stem lengths are preliminary and, therefore, should be viewed with caution. These analyses do suggest, however, that both thecal height and the number of circlets/plates are potentially good proxies for age in gogiid echinoderms.

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

In terms of interpreting the population structure and dynamics of fossil echinoderm accumulations, studies on modern communities provide an analytical framework; accumulations of small individuals with extremely similar sizes (for example, in holothurians – see Rowe, 1971, 1972; Billett and Hansen, 1982) are typically interpreted as representing a single highly synchronous reproductive event and, in general, a sedimentary environment characterized by turbidity flows and mass burials (Billet and Hansen, 1982). In contrast, two or more modes (see size-frequency analyses by Fujita and Ohta, 1990 on populations of the ophiuroid *Ophiura sarsa*) indicate a mixture of age classes. Packer et al. (1994) obtained similar results for populations of *O. sarsa* from Maine, USA, finding a distinctly bimodal distribution with a sharp peak in the frequencies of small individuals interpreted as representing a single cohort. A second, broader peak in larger individuals was interpreted as representing the accumulation of several older cohorts. The *Gogia* sp. meadow-type community reported herein is similar to those described by Fujita and Ohta (1990) and Packer et al. (1994); the population is made up of multiple size modes that likely represent several discrete age classes. This in turn suggests that the immediate palaeoenvironment was relatively stable, with long periods of relative quiescence (long enough to allow multiple episodes of spawning and recruitment) between catastrophic obrution and mass-burial events. In terms of fossil material, similar patterns have been documented in the edrioasteroid *Curvitriordo stecki* and were explained as the result of a hiatus in recruitment (e.g., seasonal breeding) or some other factor that greatly restricted recruitment of new larvae for a period (Sumrall, 2010; Shroat-Lewis et al., 2011).

The age structure of the studied population also allows broader inferences to be made regarding the reproductive biology of gogiid echinoderms. The identification of multiple age classes implies that the production and release of gametes was likely seasonal, leading to pulses of recruitment and settlement that were subsequently reflected in size modes. In modern continental shelf (deeper than ~ 500 m) and deep-sea communities, coordinated reproduction is triggered by a seasonal flux of organic matter and phytodetritus from surface waters (e.g., Tyler and Young, 1992; Morales-Nin and Panfili, 2005). Therefore, these data provide evidence to suggest that this flux was already well-established and a significant control on organismal biology and ecology by the middle Cambrian – a comparatively short time after the explosive increase in both the volume and character of planktonic diversity at the base of the Phanerozoic (see Butterfield, 2009, 2011).

4.4. Ontogeny

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

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

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

Several characters are positively correlated with thecal height, suggesting that they also changed during ontogeny. Stem length has the most significant correlation (Spearman's rho = 0.79, $p < 0.001$; Kendall's tao = 0.64, $p < 0.001$), implying that gogiids increased the length of the stem in concert with the size of their theca, although the mechanisms underlying the growth of these distinct elements may have been rather different. Comparing the stems of specimens belonging to different ontogenetic stages (e.g. Fig. 5A vs. 5E), it appears that they grew chiefly by incorporating new plates, but the accretion of calcite on existing ossicles probably also played a role, with the stem plates up to four times larger in the larger gogiid individuals. However, the incomplete preservation of stems in a number of the specimens (see section *4.3.*) implies that many of our measures of stem length are underestimates, and the stem may actually have grown at a faster rate than currently documented. An additional character that has a positive correlation with thecal height (albeit a weaker one), is the number of thecal plate circlets, which ranges from 5 to 11 (Spearman's rho = 0.37, $p < 0.01$; Kendall's tao = 0.29, $p < 0.01$). This may have been one further mechanism by which gogiids were able to increase the size of their theca during development.

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

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

Parsley and Zhao (2006) showed that the number of brachioles increased during gogiid ontogeny, and this fits with our findings for *Gogia* sp.; the number of brachioles is positively correlated with thecal height (Spearman's rho = 0.54, $p < 0.001$; Kendall's tao = 0.42, $p < 0.001$). A model for ambulacral development based on edrioasteroids suggests that the first ambulacra to form were the lateral branches BC and DE, followed by A, and ending with the branching of the lateral branches into separate B, C, D and E (Sumrall and Wray, 2007). Similar patterns have been observed in gogiids, resulting in the formation of five ambulacra and five brachioles (Parsley and Zhao, 2006). It has been suggested that the increase in the number of brachioles after the acquisition of five-fold symmetry was triggered by a change from simple ambulacra to heterotomous ambulacra, together with a subsequent increase in the number of facets for the attachment of brachioles located at the end of each ambulacral branch. This model provides a clear picture of when during ontogeny the number and size of brachioles increased but does not inform on whether brachioles grew through the addition of new plates or by increasing the size of existing ones. There is no significant correlation between thecal height and the number of brachiolars per two millimetres in the proximal part of the brachioles, demonstrating that these plates did not increase in size during ontogeny. Therefore, the increased size of brachioles in adult gogiids is most probably the product of adding new plates in their distal parts.

To sum up, different mechanisms controlled development in different parts of the gogiid skeleton. The theca grew through the addition of new plates but also by accretion of calcite on existing plates. The stem grew through a similar mechanism to the theca, chiefly by adding new plates, but also through increasing the size of the existing ossicles. Whether the new elements were added at the stem–theca contact, or intercalated along the stem length, is not something we can unambiguously address based on our material; however, the presence of primary stem plates bounded by small secondary elements in larger specimens points to the later mechanism as the most plausible. The brachioles grew through the addition of new plates in their distal parts, and there is no evidence that additional plates were inserted along their length, or that plate sizes increased with ontogeny.

4.5. Taxonomic recommendations

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

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

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

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Figure and table captions

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

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

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

orientations, which were used to build the rose diagram in Fig. 1. B. Complete specimen showing the diagnostic characters of eocrinoids. Abbreviations: brs, brachioles; th, theca; st, stem; hd, holdfast. C–E. A number of specimens showing a range of sizes and orientations. All photographs are from latex casts whitened with NH_4Cl sublimate.

Fig. 4. Growth series of *Gogia* sp. A. Smallest specimen with a thecal height of 0.27 cm, very few brachioles and a wide and short stem. B. Specimen with a thecal height of 0.39 cm and a longer and thinner stem. Theca composed of only primary thecal plates. C. Specimen with a thecal height of 0.53 cm, showing multiple brachioles and with secondary thecal plates starting to appear between plate junctures. D. Specimen with a thecal height of 0.58 cm in which the first small epispires start to appear close to the thecal summit. E. Specimen with a thecal height of 0.83 cm. F. Specimen with a thecal height of 0.81 cm. G. Specimen with a thecal height of 0.87 cm, showing the generation of new thecal plates on the left side. H. Specimen with a thecal height of 0.93 cm. I. Specimen with a thecal height of 0.93 cm in which epispires start to appear in the upper portion of the theca. J. Two specimens with thecal heights of 0.82 and 0.99 cm. K. Specimen with a thecal height of 0.93 cm in which very small epispires start to appear in the middle part of the theca. L. Relatively large specimen with a thecal height of 1.4 cm in which epispires are absent in the middle part of the theca, even though they are present in other specimens with a similar size. M. Large specimen with a thecal height of 1.72 cm and an atypical distal end of the stem. N. Large specimen with a thecal height of 1.73 cm and with epispires present in the upper three-quarters of the theca and with abundant brachioles. All photographs are from latex casts whitened with NH_4Cl sublimate.

Fig. 5. Morphological variation in the stem of Gogia sp. A. Very short stem of an early juvenile with a thecal height of 0.27 cm. B. Two stems with distal curved parts. C. Stem from a relatively large specimen showing S-shaped curvature. D. Strongly bent stem. E. Normal stem with a distal attachment structure; compare with the stem of an early juvenile in A. F. Stem with a distal loop. All photographs are from latex casts whitened with NH_4Cl sublimate.

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

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

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

Fig. 9. Details of the theca for three different ontogenetic stages in *Gogia* sp. A. Specimen with a thecal height of 0.39 cm showing few plate circlets, large primary thecal plates and very small epispires in only the uppermost part of the theca. B. Specimen with a thecal height of 0.81 cm showing more thecal plates than in the previous stage and with new plates appearing in plate junctures; epispires occur in the upper part of the theca, close to the summit. C. Specimen with a thecal height of 1.73 cm and a theca composed of mostly large thecal plates and with epispires present in the upper three-quarters of the theca. All photographs are from latex casts whitened with NH_4Cl sublimate.

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

Appendix A. Supplementary data

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

Supplementary Video 1. Video showing the studied slab and latex casts of different specimens of *Gogia* sp.

Supplementary Table 1. Measurements and morphological data for specimens of *Gogia* sp. For individual specimen numbers, see Supplementary Fig. 1.