



The nature of the platyceratid–crinoid association as revealed by cross-sectional data from the Carboniferous of Alabama (USA)

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Abstract

The association of Paleozoic crinoids and platyceratid gastropods has drawn the attention of paleontologists for nearly 200 years. It has been variably interpreted as predatory, commensalistic, mutualistic or parasitic. Previous cross-sectional analyses of large populations of crinoids and platyceratids have favored the parasitic explanation for the interaction because of data suggesting that the average size of infested crinoids is less than that of their uninfested conspecifics. In this study, we examine a population of *Dizygocrinus* from the Carboniferous (Early Viséan) Monteagle Limestone of Madison County, Alabama, USA. Of the 198 specimens examined from a single lens, 37 showed evidence of infestation by way of attached gastropods or drillholes at the base of their anal tubes—slender, cylindrical extensions of the tegmen with the periproct at the distal end. In contrast to the results of previous studies, the average size of the infested *Dizygocrinus* in this study was greater than that of the uninfested subset. Using conceptual and numerical models, we demonstrate that despite the slightly larger average size of the infested crinoids, the gastropods diminished the growth rates of their hosts. Thus, parasitism is the best explanation for this biotic interaction. The presence of an anal tube among the Monteagle Limestone *Dizygocrinus* may have diminished the negative impact of their parasites by increasing the length of the hindgut, and as a consequence, increased crinoids' ability to absorb nutrients.

Keywords Kleptoparasitism · Gastrophagy · Numerical modelling · Size distribution

Introduction

The well-known association between platyceratid gastropods and crinoids is one of the longest lasting (Ordovician to the Permian) examples involving live–live interactions among Paleozoic macroinvertebrates. The occurrence of platyceratids attached to crinoid calyxes has been reported in the literature since the middle of the nineteenth century and has been the subject of various interpretations (see Bowsler 1955; Gahn and Baumiller 2003, 2006; Keyes 1888 for period reviews). A popular

early hypothesis considered crinoids to be predatory on platyceratids, fossilized in the act of consuming their prey while holding onto it with their arms (Austin and Austin 1843; White 1863). Meek and Worthen (1866) rejected the predatory interpretation by noting that the close match between the apertural margin of the gastropods and the morphology of crinoid calyxes implied ontogenetic persistence of the interaction. They subsequently argued that gastropods may have fed on “the numerous little organisms brought in by the action of cilia, along the ambulacral furrows of the arms of the Crinoids, or in currents produced by the motions of the arms of the latter” (Meek and Worthen 1873, p. 339). Soon thereafter, what was to become the preferred interpretation emerged, that of coprophagy (e.g., Hinde 1885). In this scenario, the gastropod positioned itself over the crinoid anal opening and lived there semi-permanently while feeding on the crinoid's excrement. The location of the gastropod, its tight fit to the calyx, and its growth lines reflecting modification of the aperture to accommodate its own changing size, as well as that of its substrate (the crinoid), were all consistent with coprophagy.

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Many additional examples of platyoceratids attached to crinoids have been documented since coprophagy became the standard interpretation near the end of the nineteenth century and the vast majority of those share the classic features. The standard interpretation of coprophagy assumes that whereas the gastropods must have gained an advantage by infesting their host, their presence was either neutral or even beneficial to the crinoids they infested (Bowsher 1955; Keyes 1888; Kluessendorf 1983; Lane 1978; Meyer and Ausich 1983; Wood 1980). However, some authors have suggested that the relationship may have been detrimental to crinoids. For example, Lane (1984) argued that the platyoceratids were gametophagous, feeding on gametes that may have been stored within crinoid calyxes and shed through their anal vents. Moreover, Rollins and Brezinski (1988) suggested that platyoceratids may have interfered with their host's feeding ability or that they were kleptoparasitic, stealing food from the arms of their hosts. Platyoceratids may have also been gastrophagous, a specific type of kleptoparasitism characterized by the stealing of partially digested or undigested food directly from the gut, most likely the hindgut or foregut (Baumiller 2002, 2003; Baumiller and Gahn 2002; Baumiller et al. 2004; Gahn and Baumiller 2003, 2006; Gahn et al. 2003; Haugh 1975). The latter hypotheses, physical interference with the crinoids' feeding ability and kleptoparasitism, make explicit predictions about the impact of the platyoceratids on the growth rates of their hosts: A crinoid infested by a platyoceratid is expected to grow at a slower rate than an uninfested conspecific. Such an effect has been documented for the modern capulid gastropod, *Trichotropis cancellata*, which infests filter feeding serpulid worms and steals their food (Iyengar 2002). Iyengar's longitudinal study has convincingly demonstrated that infested serpulids grow more slowly than uninfested individuals from the same population. Unfortunately, longitudinal data are not available in the case of platyoceratids and crinoids as fossil crinoids cannot be aged; so, cross-sectional data have been used instead. Two studies which employed the cross-sectional approach found that in several camerata populations, infested crinoids were on average smaller than their uninfested conspecifics suggesting lower growth rates among platyoceratid-infested crinoids (Gahn and Baumiller 2003; Rollins and Brezinski 1988).

A detrimental effect of platyoceratids on the crinoids they infest is also explicit in the "targeting" hypothesis (Brett 2003; Brett and Walker 2002; Brett et al. 2004), which states that the presence of epibionts attracts predators to the hosts of the infesters. Attacks on crinoid epibionts, including platyoceratids, would have resulted in collateral damage to crinoids, either in the form of non-lethal injury or death. Spines found on some crinoids could have repelled predatory attacks; indeed, the positive correlation

between tegmen spines and platyoceratids is consistent with the interpretation of spines as anti-predatory adaptations and also the targeting hypothesis (Syverson et al. 2018).

In this study, we further explore the nature of the platyoceratid–crinoid association by focusing on a single species of camerata crinoid from the Carboniferous (Late Viséan) of Alabama. This population of infested crinoids is particularly interesting given that its members possess a long anal tube (see below), a structure hypothesized to have evolved in response to platyoceratid parasitism (Keyes 1888). These specimens of *Dizygocrinus* facilitate the first study of a large, single population of tubed camerates that are infested by platyoceratids. We use data on the position of platyoceratids, and the relative sizes of the crinoids and their infesters, in combination with heuristic and numerical models, to test whether this interaction is best characterized as commensalism (e.g., coprophagy) or parasitism (e.g., gastrophagy).

Platyoceratids and camerata crinoids

The subclass Camerata is a diverse clade of Paleozoic crinoids ranging from the Lower Ordovician to the Permian (Ubahgs 1978; Wright et al. 2017). Over 300 genera of camerates appear in Webster's compendium (Webster and Webster 2014). Camerates are by far the most commonly infested crinoids: Of 61 crinoid genera associated with platyoceratids, 41 are camerates (Gahn and Baumiller 2006), a preference that is statistically significant (Chi squared: $P < 0.001$). The high food gathering ability of camerates due to their many, densely pinnulate arms has been suggested as one possible reason why they may have been the favored hosts of infesting platyoceratids (Baumiller 2003). Yet, not all camerates were preferred equally by platyoceratids. Approximately 20% of camerata genera possessed a pronounced chimney-like structure, which is a slender, multi-plated extension of the tegmen with the anus at its distal tip (Fig. 1). An analysis of platyoceratid infestation of tubed and tubeless camerates collected from two Carboniferous formations, the Lake Valley Formation (New Mexico, USA) and the Burlington Limestone (Iowa, USA), revealed significantly lower infestation frequencies among tubed camerates (Gahn and Baumiller 2006). This suggests that the tube was likely a deterrent to infesting platyoceratids.

In what way would the tube function as a deterrent? If platyoceratids were strictly coprophagous, a plausible argument is that the small distal apex of the tube would have been difficult to settle upon and may have limited the size that platyoceratids could have attained without impairing their hosts. In fact, we are unaware of a single example of a platyoceratid, either small or large, attached to

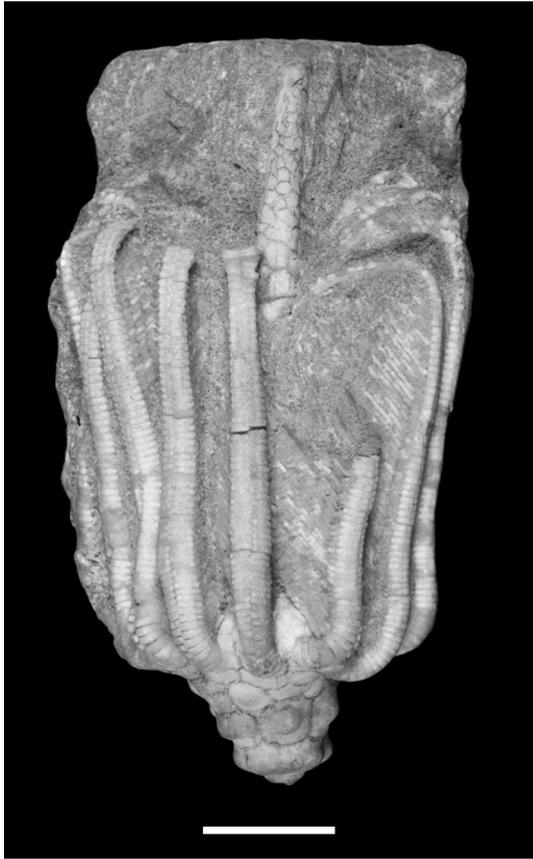


Fig. 1 An example of a tube-bearing camerate, *Macrocrinus verneuillianus* (USNM S807), from the Burlington Limestone, Carboniferous, Iowa, USA. Scale bar 10 mm

the tip of a camerate tube. Instead, platyceratids are found at the base of the tubes, directly on the tegmen (Baumiller 1990; Gahn and Baumiller 2006; Keyes 1888; Van Sant and Lane 1964; Wachsmuth and Springer 1897). This position is inconsistent with strict coprophagy and indicates a different trophic strategy for the infesting platyceratids. Van Sant and Lane (1964, p. 34) argued that these gastropods could “burrow [sic, bore] into the crinoid”, and indeed, platyceratid drilling abilities were demonstrated by serially sectioning a specimen of the Carboniferous camerate *Macrocrinus*: A drillhole was found at the base of its tube, directly beneath the infesting gastropod (Baumiller 1990). Drillholes produced by platyceratids are now known in numerous camerates (Baumiller 1990; Baumiller et al. 2004; Gahn and Baumiller 2006; Gahn et al. 2003), including those analyzed in this study (Fig. 2). This growing list of examples demonstrates that drilling behavior was a pervasive strategy employed by the platyceratids that infested tube-bearing camerates.

By drilling the tube at its base, platyceratids were, by definition, causing injury to their hosts, but more importantly, they could penetrate the calyx wall, thereby



Fig. 2 An example of a drillhole at the base of the anal tube of *Dizygocrinus* from the Monteagle Limestone. Scale bar 5 mm

accessing food captured by the crinoids, their soft tissues and possibly gametes. While knowledge of platyceratid anatomy would be required to assess how far their proboscises could reach into the interior of their hosts (see Sutton et al. 2006), even a short proboscis could have interfered with the normal passage and assimilation of nutrients moving through hindgut. This would constitute a detrimental interaction and negatively affect the host’s energy budget. One prediction of such an effect would be reduced growth rates of infested crinoids relative to uninfested conspecifics. We test this prediction by examining cross-sectional data and comparing the size distribution of uninfested (Fig. 3a) and infested (Fig. 3b) specimens of *Dizygocrinus*.

Materials and methods

The crinoids under consideration were collected from a single lens of shale and partially silicified packstone in the lower part of the Monteagle Limestone (Carboniferous, Upper Viséan), Redstone Arsenal, Madison County, Alabama (34°40′27.84″N, 86°39′5.47″W). Although most of the specimens were collected as isolated calyces, they were originally preserved with arms and stems in a large tangled mass that was buried by an obrution event. However, because most of the crinoids were preserved in a muddy matrix that weathers very readily, most of the specimens

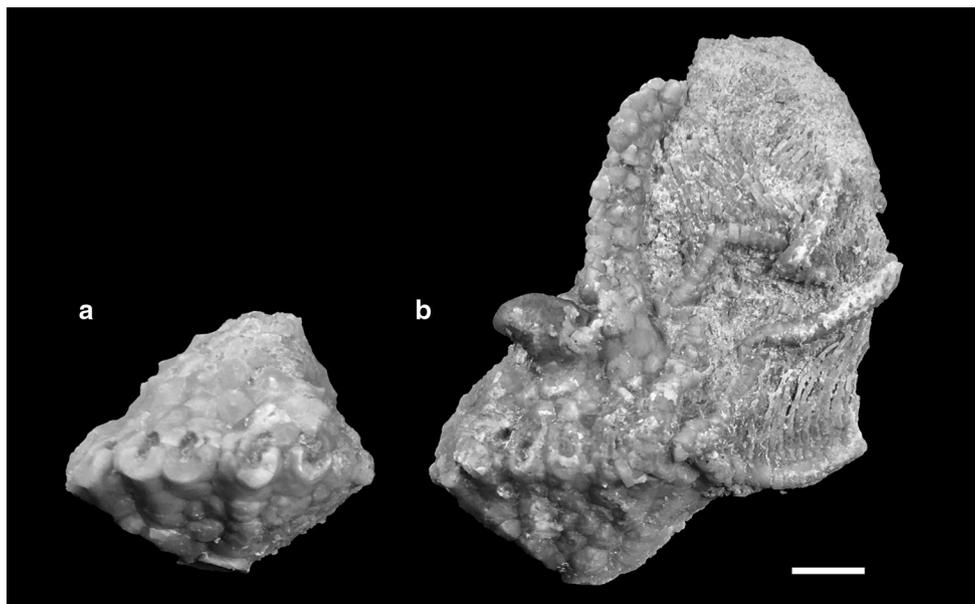


Fig. 3 Examples of platyceratid-uninfested (a) and -infested (b) specimens of *Dizygocrinus* from the Monteagle Limestone. Scale bar 5 mm

fell apart as they were exposed at the surface of the outcrop.

Although numerous crinoid taxa (e.g., *Heliosocrinus* and *Phacelocrinus*) and other marine invertebrates were found in the deposit, the lens was largely dominated by a single species of tubed camerate, commonly referred to as *Batocrinus persculptus* by Alabama fossil collectors. However, there is much confusion surrounding the taxonomy of this species. It was originally described by Ulrich (1917) under the genus *Dizygocrinus* and, although Ulrich figured the species, he failed to provide a description. Lane (1963) synonymized the species with *Batocrinus unionensis* Worthen, 1890, whereas Webster and Webster (2014) listed the aforementioned species as belonging to the genus *Globocrinus*, which is why we, in an earlier abstract (Gahn et al. 2015), referred to the Monteagle Limestone specimens as *Globocrinus unionensis*. After carefully examining the crinoids, that assignment is incorrect.

When Worthen (1890) established *B. unionensis*, he figured specimens from two distinct species, one of which is now considered to be *G. unionensis*, the other *Dizygocrinus davisi* (Rowley and Hare 1891; see Ausich 2009; Ausich and Kammer 2010 for further discussion). Thus, *G. unionensis* is also synonymized with *D. davisi* in Webster's compendium (Webster and Webster 2014). However, as is true for *G. unionensis*, the Monteagle Limestone batocrinids do not conform convincingly to the species concept of *D. davisi*.

For the purposes of this study, it is crinoid morphology and the distribution of platyceratids, not alpha taxonomy, which are of greatest import. Considering the morphology

of the specimens used in this study, the most recently published genus concepts for batocrinids (Ausich and Kammer 2010), and the confusion surrounding the species-level taxonomy of these specimens, we simply refer to the specimens addressed in this paper as *Dizygocrinus*.

We examined 198 specimens of *Dizygocrinus* from the Monteagle Limestone. With few exceptions, all individuals were represented by loose calyces lacking arms and stems. As mentioned above, all of the specimens originated from a single lens and are interpreted as representing one population with little or no time-averaging. Mostly due to post-depositional compaction of the muddy matrix, many of the specimens were compressed, some extremely so. This prevented us from consistently measuring the height of the calyces; thus, we used the width of the radial plates, measured with digital calipers, as a proxy for body size. In addition, we assessed the taphonomic grade of each specimen, considering both the degree of compaction and disarticulation of each calyx, on a scale from 4 (well preserved) to 1 (poorly preserved; see Gahn and Baumiller 2004). This allowed us to evaluate potential size-related taphonomic biases in our data.

Finally, we categorized each specimen by the presence or absence of an infesting platyceratid. Specimens were considered to have been infested only if a gastropod aperture was clearly attached to the crinoid tegmen or if a drillhole was present at the base of the tube. Gastropods that were associated with calyces, but not attached to hosts, were not counted as infesters. However, it is unlikely that this would have led us to misidentify infested crinoids as uninfested, given the signatures of their presence left on the hosts. Regardless, the specimens of *Dizygocrinus* from the

Monteagle Limestone represent the most heavily infested population of tubed camerates of which we are aware.

Results and discussion

The sample of *Dizygocrinus* from the Monteagle Limestone consists of 161 individuals that show no evidence of infestation and 37 (19%) infested individuals; the latter either have a drillhole or snail at the base of the tube. Using the width of the radial plate as a proxy for crinoid body size, uninfested specimens average 3.67 mm (SD 0.58) and infested crinoids average 3.95 mm (SD 0.46) (Fig. 4). The difference in means (0.28 mm) is significant ($P < 0.01$ using t test).

The size distribution of *Dizygocrinus* from the Monteagle Limestone indicates that individuals infested by platyoceratids are on average larger than the uninfested conspecifics. Although the difference in their average size is small, about 7.5%, it is nevertheless statistically significant. This result might appear to contradict the kleptoparasitic hypothesis, suggesting that infesting gastropods benefited their hosts instead of impacting them negatively. To explore this further, we present a heuristic for hosts and infesters assuming neutrality, that is, no negative or positive effect on host growth. The heuristic shows that under

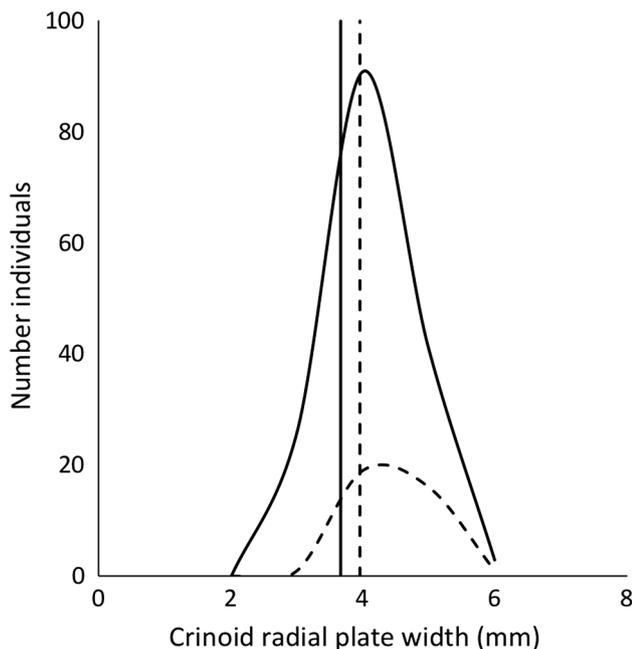


Fig. 4 Size distributions of uninfested (solid line; $N = 161$) and infested (dashed line; $N = 37$) *Dizygocrinus* from the Monteagle Limestone. Crinoid size is represented by widths of the radial plates. The average size of uninfested specimens = 3.67 mm (SD 0.58), shown as solid, vertical line and that of the infested specimens = 3.95 mm (SD 0.58), shown as dashed, vertical line

realistic, empirically based assumptions, the average size of infested and uninfested crinoids from the same population will not be the same, as one might intuitively expect, but rather that the average size of infested crinoids will be larger than uninfested ones for reasons we explain below. In addition, we present a computer model to demonstrate that reducing the size difference to the 7.5% value observed in the Monteagle Limestone *Dizygocrinus* requires a substantial decrease in the growth rates of infested individuals relative to their uninfested conspecifics. This leads us to conclude that the observed pattern is consistent with platyoceratids having a detrimental effect on their hosts by reducing the hosts' growth rates as predicted by kleptoparasitism.

Platyoceratid–crinoid association: a conceptual model

Evaluating fossil populations of crinoids and platyoceratids is complicated by the fact that we must rely on cross-sectional data in our analyses. Rather than evaluating single individuals over time or comparing individuals of the same age, our data consist of overlapping cohorts even under the best of circumstances. Thus, the expected size distribution is highly dependent upon not only the nature of the biotic interaction (e.g., commensalism vs. parasitism), but also the timing of infestation relative to the age of the hosts.

The traditional hypothesis of coprophagy for the platyoceratid–crinoid interaction infers that the infesting gastropods have no negative or positive effects on their hosts. Thus, two crinoids from the same cohort, whether they be infested or uninfested, should be the same size regardless of when in its life history the infested individual was colonized. However, a coprophagous scenario does not necessarily predict an absence of difference in the average sizes of infested and uninfested subsets from the same population of crinoids. Such a pattern would only be expected if infestation were congenital, occurring only among juveniles and never subsequently. Assuming that the population is stable (e.g., birth rate = death rate and the proportion of infesters is constant), the size distribution of infested and uninfested subsets of the population will be the same only under a model of strict congenital infestation and commensalism (neutrality).

A strict model of congenital infestation of crinoids by platyoceratids is unrealistic and unsupported by the fossil record (see Baumiller 2002). Crinoids are likely to be subjected to infestation throughout their lives, and infestation of larger individuals would be especially favored. The larger individuals in a population are more likely to be infested by platyoceratids for at least two reasons. First, larger crinoids can generally be assumed to be older

individuals, and the longer an individual persists, the more likely it will be infested. Second, larger crinoids provide larger targets (greater surface area) for settling platyoceratid larvae than do smaller members of the same population. Therefore, infested and uninfested subsets from the same crinoid population should not have similar average sizes, but rather the subset of infested crinoids should be considerably larger than the subset of uninfested crinoids.

The larger average size of the infested subset of the population will be maintained if infesters do not affect the growth rates of their hosts, as is the case of coprophagy (neutral; commensal). On the other hand, gastrophagy would lead to a decrease in the average size of infested crinoids, which would reduce the size difference between the two subsets. Nevertheless, the average size of infested individuals could still remain greater than that of the uninfested conspecifics. Only when the negative effect on the hosts' growth rate by the infesters is large enough, will the average sizes of the uninfested subset be equal to or even surpass that of the infested subset. The larger size of uninfested individuals is, therefore, the clearest indication of a detrimental impact of the infester on the host, and was the pattern found by Rollins and Brezinski (1988) and Gahn and Baumiller (2003), which led these authors to conclude that in the populations examined, infesting platyoceratids had a detrimental effect on their crinoid hosts.

As mentioned above, the published studies of cross-sectional analyses of platyoceratid–crinoid interactions revealed patterns that are most consistent with parasitism (Gahn and Baumiller 2003; Rollins and Brezinski 1988). However, data for the Monteagle Limestone *Dizygocrinus* cannot be so easily interpreted, as the small, but significantly greater, size of the infested subset of the population could imply either a positive, neutral or a detrimental relationship. Therefore, we developed a numerical model to further explore platyoceratid infestation among these tubed camerates.

Platyoceratid–crinoid association: a numerical model

Model description

In modelling the association between platyoceratids and crinoids, we made some simplifying assumptions, and relied on what is generally accepted about platyoceratids and crinoids. We selected model parameters that allowed us to reproduce the Monteagle Limestone population as observed.

In the model, at time 0, a population of crinoids consists of 198 individuals of different ages and sizes as in the population of Monteagle Limestone *Dizygocrinus*. In every subsequent time step, each crinoid can die (probability μ)

or survive to the subsequent time step (probability $1 - \mu$). If the crinoid dies, it is replaced by an uninfested juvenile—this assumes that the population is stable. Uninfested crinoids, regardless of their ages or sizes, are subject to becoming infested by juvenile platyoceratids with a probability i set so that the frequency of infested crinoids is about 19% the observed population. Crinoid and gastropod growth are governed by the von Bertalanffy (1938) equation with parameters selected to generate a range of sizes that reflect the sampled population of Monteagle Limestone *Dizygocrinus*.

Crinoid mortality in the population, regardless of cause, is time homogenous; that is, the probability of death in any time unit, μ , is constant, independent of age. The average age of crinoids in the populations is, thus, $1/\mu$.

In the model, gastropods infest crinoids as juveniles and remain sedentary, fixed to the host on which they settled, for the duration of the life of their host. Only a single gastropod can settle on each crinoid.

Each simulation was allowed to run for 500 time steps, but because the results reached a quasi-equilibrium after about 20 steps (see below), only a single time step was randomly selected to represent steps 100–500. At each time step, the following data were recorded for each live crinoid: age, size, and the presence or absence of an infesting platyoceratid. Snail size was also recorded for live and dead snails. At each time step, the following population parameters were calculated for both live and dead crinoids: (a) the number of infested individuals; (b) the average age and size of infested individuals; (c) the variance in age and size of infested individuals; (d) the number of uninfested individuals; (e) the average age and size of uninfested individuals; and (f) the variance in age and size of uninfested individuals.

Numerical model results

The population structure of the live crinoids stabilized after about 20 time steps; that is, the average size and variance of infested and uninfested crinoids reached a quasi-equilibrium. The same was true for the frequency of infestation and the size structure of live gastropods. The absolute numbers of dead crinoids and snails continued to increase with each time step, but the population structure of the death assemblage also reached a quasi-equilibrium after about 20 time steps. The population parameters of the live and death assemblages were nearly identical.

To model the coprophagous (neutral) scenario of the association between platyoceratids and crinoids, characterized by no detrimental effect on the growth rate of the host by the infester, 1000 simulations of the model were run with the same growth parameters for infested and uninfested crinoids. As the conceptual model predicted, the

numerical model results indicate that infested crinoids are on average larger than uninfested crinoids: The size ratio of infested–uninfested crinoids was 1.24 (SD 0.05). Infested crinoids were larger, on average, in all 1000 simulations. Figure 5 shows the size distributions of the infested and uninfested crinoids from one of the simulations of the neutral scenario. Even by eye, it is clear that the infested part of the population (dashed line) is shifted substantially towards larger sizes. When compared to the observed size distributions of infested and uninfested *Dizygocrinus* (Fig. 4), the differences between the two are notable. Although infested crinoids are significantly larger than uninfested conspecifics in both the observed and simulated distributions, the ratio of infested–uninfested *Dizygocrinus* is only 1.07 in the observed data, much smaller than in the modelled neutral scenario (1.24). Again, this can be seen visually by comparing the differences in the modes of the infested and uninfested populations in Figs. 4 and 5. In the former (*Dizygocrinus* observed), the modes are much closer to each other than in the latter (*Dizygocrinus* modelled). This indicates that the growth rates of the infested Montea Limestone *Dizygocrinus* are much lower than expected given the behavior of the model. Therefore,

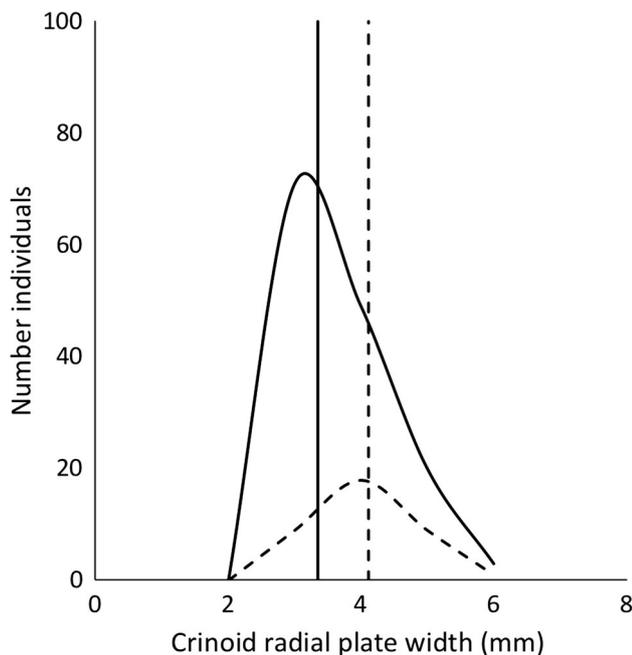


Fig. 5 Size distributions of uninfested (solid line) and infested (dashed line) crinoids from one simulation of the neutral scenario (growth rate infested = growth rate uninfested). In this simulation, there were 37 uninfested (average size = 4.12 mm; SD 0.61; solid, vertical line) and 143 infested (average size = 3.35 mm; SD 0.52; dashed, vertical line) specimens. Values used in simulation: $m = 0.1$; $i = 0.025$; von Bertalanffy parameters S_{∞} (asymptotic size) = 6; b (scaling factor) = 0.67; K (rate at which asymptotic size is approached) = 0.05. See “Appendix” for details of the von Bertalanffy equation

despite the average size of infested *Dizygocrinus* being larger than their uninfested conspecifics, the observed pattern is consistent with a reduction in growth rates among infested crinoids as predicted by kleptoparasitism. To explore this further, we conducted several experiments by running simulations in which growth rates of infested crinoids were progressively reduced relative to uninfested conspecifics.

The results of those experiments (Fig. 6), representing neutrality and five instances of increasingly severe parasitism, are shown as the ratio of the average size of infested–uninfested subsets of crinoid populations (y-axis) against the ratio of their modelled growth rates (x-axis). Under the neutral scenario (solid circle), where the growth rates are the same (ratio = 1), the size ratio of infested–uninfested crinoids is 1.24, as discussed above; the vertical bars represent the ± 1 standard deviation of the ratio obtained from 1000 simulations. The average size ratio under the neutral scenario is, thus, significantly higher than the size ratio observed for the Montea Limestone *Dizygocrinus* (1.07, represented by the solid horizontal line in Fig. 6).

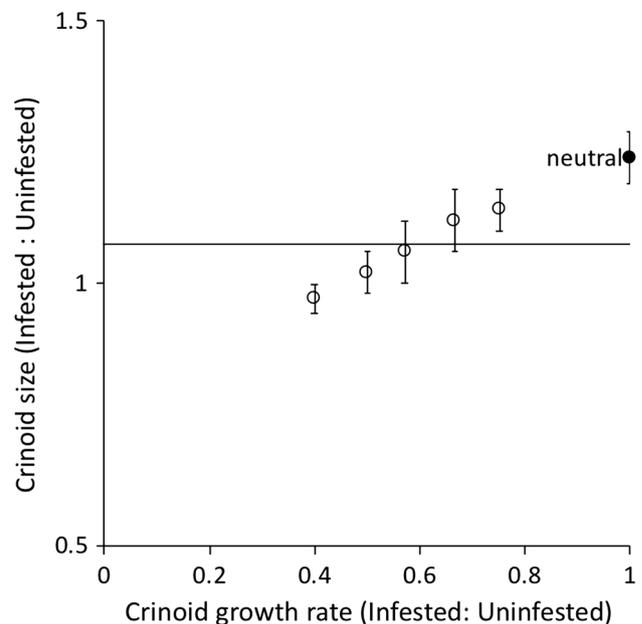


Fig. 6 Ratio of sizes of infested–uninfested crinoids as a function of the nature of the association between platyceratids and crinoids expressed as the impact of the infesting platyceratid on the growth rate of its host (growth rate of infested crinoid: growth rate of uninfested crinoid). The average ratio of infested–uninfested crinoids (± 1 standard deviation) obtained from 1000 simulations; neutral scenario = solid circle (infested growth rate = uninfested growth rate); detrimental scenarios = open circles (infested growth rate < uninfested growth rate). The ratio of infested–uninfested crinoids in the Montea Limestone *Dizygocrinus* (1.07) is represented by the solid horizontal line

The size ratio of infested–uninfested Montea­gle Limestone *Dizygocrinus* is consistent with simulated growth rates of infested crinoids that are only 0.67–0.5 of growth rates of uninfested conspecifics (Fig. 6). This suggests that the platyceratids infesting the Montea­gle Limestone *Dizygocrinus* exacted a substantial toll on their hosts, decreasing their growth rates by 33–50%. Whether this can be attributed entirely to gastrophagy by the platyceratids is uncertain as these gastropods are likely to have had other deleterious effects on their host as discussed previously. Nevertheless, this analysis does support the hypothesis that the interaction between Montea­gle Limestone platyceratid gastropods and *Dizygocrinus* is better characterized as parasitism than as commensalism. As the model developed here is quite general, applicable to any non-congenital association between a host and an infester, we are eager to have it applied to other platyceratid–crinoid associations for which population sizes are sufficiently large and other assumptions are met (see “Model description”).

Caveats

In the numerical models, we used a range of values for most of the parameters, including the mortality rate, μ , infestation rate, i , as well as the growth parameters in the von Bertalanffy equation. The values used were constrained by some of the properties of the observed Montea­gle Limestone *Dizygocrinus*, such as the total size of the crinoid population (198), the proportion of infested crinoids (19%), and the size ranges of the crinoids and their infesters. However, there are very many combinations of the values of these parameters that can satisfy the constraints, and we have explored but a few. Nevertheless, in the combinations we examined, we discovered no results for the neutral (commensalistic) or detrimental (parasitic) scenarios that were substantially different from what we reported.

One assumption critical to modelling the platyceratid–crinoid system, or any other infester–host system, is the mode and timing of infestation. As we discussed in the section highlighting the conceptual model, strict congenital infestation of commensalistic platyceratids on their hosts leads to identical size distributions among infested and uninfested crinoids. Based on the conceptual model and empirical evidence, we argued that the association between platyceratids and crinoids is not congenital; thus, infested crinoids should be larger than their uninfested conspecifics. In the numerical simulations, we chose to model infestation as random with respect to the size of the crinoid—the probability of platyceratid infestation was size independent. While random infestation is certainly non-congenital, it is but one of many non-congenital infestation scenarios.

For example, infesters may prefer either smaller or larger hosts.

We chose a size-independent infestation model for two reasons. First, a model of random infestation requires the fewest assumptions. Second, an analysis of the relative sizes of the Montea­gle Limestone *Dizygocrinus* and their platyceratid hosts were not strongly correlated. If the Montea­gle Limestone platyceratids preferentially selected small crinoids, there should be a tight correlation between the size of a host and its infester: Small crinoids should only be associated with juvenile platyceratids and large crinoids with adult platyceratids. Admittedly, because of taphonomic limitations, our sample size is relatively small ($N = 8$), but in the data available from the Montea­gle Limestone, the relationship between hosts and infesters is positive (Fig. 7), although the slope of the regression is not significantly different from 0 ($P = 0.056$).

A further test of host selectivity on the Montea­gle Limestone *Dizygocrinus* was conducted by running the model under three scenarios: (a) preferential infestation of smaller crinoids ($i \propto 1/\text{crinoid size}$); (b) preferential infestation of larger crinoids ($i \propto \text{crinoid size}$); and (c) random infestation (i independent of crinoid size). We

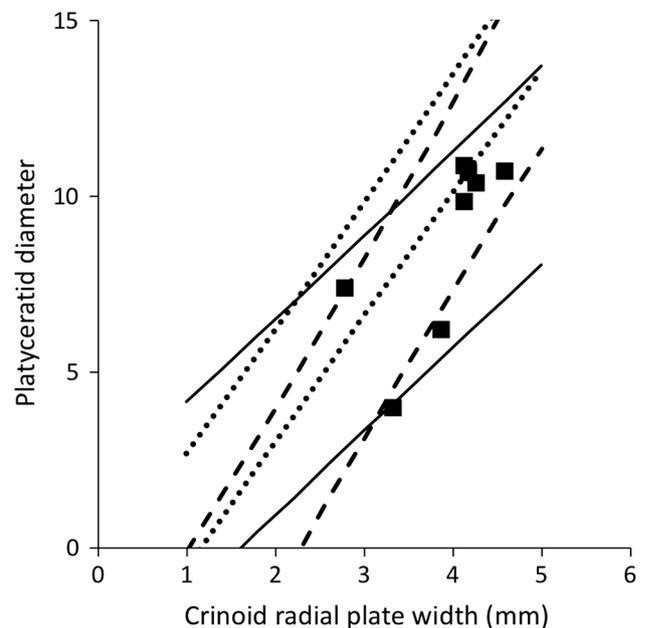


Fig. 7 The 95% predictions intervals (PI) for the relationship between the size of an infesting platyceratid and its crinoid host obtained from 1000 simulations of the platyceratid–crinoid association under 3 infestation scenarios: (1) preferential infestation of smaller crinoids ($i \propto 1/\text{crinoid size}$), 95% PI falls between dotted lines; (2) preferential infestation of larger crinoids ($i \propto \text{crinoid size}$), 95% PI falls between dashed lines; and (3) random infestation (i independent of crinoid size): 95% PI falls between the solid lines. Observed data from Montea­gle Limestone on the relationship between the size of platyceratid and their *Dizygocrinus* hosts are represented by the solid black squares

ran 1000 simulations for all three scenarios, generating 95% prediction intervals (PI) for each scenario (Fig. 7). The observed data for the Monteagle Limestone *Dizygocrinus* overlap all three sets of prediction intervals, but they do not fit either of the host selectivity scenarios as well as that of random infestation, as they all fall within the 95% PI only for the latter scenario. While this test is clearly limited given the small size of the sample, it nevertheless guided our decision to use a size-independent infestation model.

In our analyses we implicitly assumed that the Monteagle Limestone data are not biased in ways that would impact the results. However, it is important to consider potential taphonomic and sampling biases. As discussed above, most of the specimens in this study were collected as loose calyxes despite being preserved as relatively complete specimens. This allowed us to see snails and drillholes that might have been otherwise obscured by matrix or the crinoids' arms. However, the severe compression characteristic of many of the specimens, both crinoids and platyceratids, and the time they sat weathering on the surface, likely resulted in the disassociation of some platyceratids and their hosts. One reason we were not able to examine the size relationships between many of the crinoids and their infesters is that the snails were so badly fragmented that we could not adequately measure them. Snails were likely disassociated from their hosts as they weathered on the surface, as indicated by the many isolated platyceratids in the deposit, in addition to disassociating from their hosts during the trauma associated with the obrution event. However, it is unlikely that this would have led us to misidentify infested crinoids as uninfested, given the signatures of their presence left on the hosts.

Compression of the fine-grained matrix entombing the crinoids also produced potential biases. The degree of calyx compression and associated disarticulation is not random with respect to size. Splitting the Monteagle Limestone *Dizygocrinus* into two groups based on mean radial plate width reveals that crinoids below mean body size exhibit a significantly lower degree of compaction and disarticulation than their larger conspecifics ($P < 0.05$, see Gahn and Baumiller 2004 for methods). If this resulted in larger infested crinoids becoming dissociated from their infesters and being misidentified as uninfested, that would artificially reduce the observed difference in average size of infested and uninfested crinoids, making the neutral scenario easier to reject. On the other hand, infestation may bind the host's plates and make infested specimens less prone to disarticulation, which would artificially increase the observed difference in average size of infested and uninfested crinoids, making the neutral scenario more difficult to reject. We are currently unable to quantitatively assess these two sources of plausible bias.

Conclusions

Biotic interactions in the geologic past are difficult to unravel, yet because they provide insights into various aspects of the ecology and evolution of extinct organisms (e.g., Vermeij 1987), they are surely worth exploring. The association between platyceratid gastropods and crinoids persisted from the Ordovician to the Permian, and was sufficiently common to have left a rich fossil record; so, it is not surprising that it has attracted the attention of paleontologists for nearly two centuries. Concepts about the nature of this interaction have evolved through the decades: from crinoids being viewed as predators, and, thus, benefiting from the interaction (e.g., Austin and Austin 1843); to crinoids serving as the hosts of coprophagous gastropods that did not impact them negatively and may have even aided them by preventing crinoids from fouling themselves (e.g., Bowsher 1955); and, finally, to crinoids being harmed by platyceratids via physical interference, kleptoparasitism or even by attracting the attention of unwanted predators (e.g., Brett 2003; Gahn and Baumiller 2003). While appealing, many of these concepts have proven difficult to test and, thus, have remained largely in the realm of speculation. In this study, we developed explicit predictions about the impact on crinoid growth rates implicit to hypotheses of commensalism and parasitism. We focused our efforts on a cross-sectional analysis of tubed camerates that were infested by platyceratids. In such associations, platyceratids are positioned at the base of the crinoid anal tube, away from the periproct, and thus, strict coprophagy can be rejected.

Drillholes beneath infesting platyceratids indicate that they were in a position to gain access to partially digested nutrients in the crinoid hindgut and, possibly, even undigested nutrients in the foregut (Haugh 1975). This suggests that the platyceratids could primarily target food gathered by their hosts. However, if Lane (1978) was correct in suggesting that camerates stored their gametes within their calyxes, platyceratids were equally well positioned to steal gametes that would have likely passed through the camerates' anal tubes. If platyceratids were indeed kleptoparasitic, infestation should lead to lower growth rates in their crinoid hosts, and our conceptual and numerical models illustrate how such an effect would be expressed in subpopulations of infested and uninfested crinoids. Data on the size distribution of infested and uninfested *Dizygocrinus* from the Monteagle Limestone show a pattern consistent with the predictions of kleptoparasitism.

These findings support previous studies which have concluded that platyceratids were crinoid parasites (Baumiller 1990, 2003; Baumiller et al. 2004; Baumiller and Gahn 2002; Gahn and Baumiller 2003, 2006; Gahn et al.

2003, 2015; Rollins and Brezinski 1988; Keyes 1888; Meek and Worthen 1866). In addition, this study lends support to the hypothesis that camerate anal tubes evolved in response to parasitic platyoceratids (Keyes 1888). As discussed previously, Gahn and Baumiller (2006) demonstrated that the tube presence diminishes infestation rates despite the drilling abilities of platyoceratids. In addition to being an effective deterrent to infestation, the tubes could have also minimized the negative effects of parasitism.

The results of previous cross-sectional studies of infested and uninfested crinoid populations were performed on crinoids without anal tubes (Gahn and Baumiller 2003; Rollins and Brezinski 1988). In those studies, infested crinoids were significantly smaller than uninfested conspecifics. In our analysis of Montea Limestone *Dizygocrinus*, the first cross-sectional analysis of tubed camerates, infested specimens are significantly larger than their uninfested conspecifics. This suggests that the growth rates of crinoids with tubes were less severely affected by parasitic platyoceratids than the growth rates of crinoids without tubes. Thus, the tube presence appears to have minimized infestation rates and also reduced the deleterious effects of parasitism. One explanation for this observation is that the lengthening of the hindgut within the long anal tubes permitted greater nutrient absorption.

Despite growing evidence for the parasitic behavior of platyoceratids, we must be careful about overgeneralizing the nature of their interactions with crinoids. It is conceivable that these interactions, which began in the Ordovician and lasted for over 200 million years, may have begun as commensalistic interactions and only later did some lineages adopt a parasitic lifestyle. Moreover, single platyoceratid species may have engaged in multiple trophic strategies, including on organisms other than crinoids. The situation is further complicated by the uncertain family-level taxonomy of platyoceratids and questions regarding the monophyly of the group (Frýda et al. 2009). The absence of robust phylogenies for crinoids and platyoceratids also makes it difficult to test evolutionary scenarios that such interactions might engender. For example, it is plausible that an antagonistic interaction, such as kleptoparasitism, could lead to escalation between host and infester. Spines and tubes could have evolved among crinoids as an adaptive response to platyoceratid parasitism. In turn, infesting platyoceratids could have overcome these defenses through strategies such as drilling or chemically inhibiting plate growth in their hosts. Testing for such evolutionary arms races demands robust phylogenies for these groups and should be a compelling incentive for more research into the phylogeny and paleoecology of crinoids and platyoceratids.

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Appendix

$$S_t = S_\infty(1 - be^{-Kt}),$$

where S_t is size at time t , S_∞ is asymptotic size, b is a scaling factor equal to $(S_\infty - S_R)/S_\infty$, S_R is size at recruitment, K is measure of rate at which organism approached asymptotic size.

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