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Evaluating the interaction between platyceratid gastropods and crinoids: a cost–benefit approach

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Abstract

The association of platyceratid gastropods and crinoids is preserved in the fossil record of the Ordovician through the Permian. The association has been generally interpreted as involving coprophagy, although recent suggestions of gametophagy and kleptoparasitism are supported by new data. Whether platyceratids were coprophagous, gametophagous, or kleptoparasitic, they would have had to obtain their energy from the crinoid without killing it. Under that scenario, the sum of nutrients captured by the crinoid would have had to support the host and the infestor. This is explored quantitatively using a cost–benefit analysis. The results suggest that (1) some crinoids were well capable of capturing sufficient nutrients to fulfill their metabolic needs as well as those of the infesting platyceratids, (2) the preference of platyceratids to infest pinnulate crinoids rather than non-pinnulate crinoids is consistent with the cost–benefit analysis, (3) under most circumstances, a parasitic strategy of platyceratids would have provided them with a greater energetic return than would a predatory strategy.

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1. Introduction

One of the classic examples of biotic interactions preserved in the fossil record is that between platyceratid gastropods and crinoids (Fig. 1). Specimens of platyceratid gastropods found attached to the calyxes of crinoids have been reported in the literature since the mid-19th century (Austin and Austin, 1843; Yandell and Shumard, 1847; Owen, 1862; Meek and Worthen, 1866).

Even these early paleontologists recognized that gastropods and crinoids must have been interacting during life, although establishing the nature of the interaction proved more elusive.

Austin and Austin (1843) argued that the specimens represented crinoids caught in the act of feeding on gastropods, offering one of the first interpretations of the interaction. Meek and Worthen (1866, 1868), who noted that the irregular shape of the gastropod margin and the tight fit it formed with the crinoid calyx required a long-term interaction, challenged the predatory interpretation; they concluded that gastropods were using crinoids as substrate. This interpretation was further elaborated when it was realized that

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gastropods typically occupy a position over the crinoids' anal aperture, and thus may have relied on crinoids for nutrients through coprophagy (Hinde, 1885; Keyes, 1888a,b).

The 'platyceratid as coprophage' interpretation persisted through much of the 20th century (e.g. Clarke, 1908, 1921; Bowsher, 1955; Lane, 1978; Meyer and Ausich, 1983; Boucot, 1990). It assumed that the coprophagous habit of platyceratids was not detrimental to the crinoid host. Recently a number of studies, including those of Lane (1984), Rollins and Brezinski (1988), Baumiller (1990, 2002), Baumiller and Gahn (2002), and Gahn and Baumiller (2003) have argued that the relationship was not neutral but rather detrimental to the host. Lane (1984) noted that whereas modern crinoids use modified pinnules as gamete-shedding structures, Paleozoic crinoids lacked such pinnules and shed their gametes through the anal vent; he suggested that under such a scenario platyceratids would have been gametophagous on crinoids. Rollins and Brezinski (1988) found that gastropod-infested crinoids were smaller than uninfested ones and Gahn and Baumiller (2003) showed that this difference was statistically significant for two species of Devonian crinoids. The smaller size of infested crinoids suggests that platyceratids may have stolen nutrients from crinoids (kleptoparasitism) or fed on their body fluids and/or soft tissues; in either case, or in the case of gametophagy, the presence of the gastropods must have been detrimental to the host crinoid.

The strict coprophagy interpretation has been further challenged by evidence of drilling of crinoids by the infesting platyceratids. This was first reported by Baumiller (1990), who found a drill-hole penetrating the test of a Mississippian crinoid directly beneath an infesting platyceratid. In that instance, the crinoid possessed a long, slender anal tube, with the anus located at the apex and the platyceratid positioned at the base of the tube, several centimeters below the anal opening. The conical hole penetrating the base of the tube directly beneath the gastropod was nearly identical in shape, size, and position to holes found in over 50 specimens of another Mississippian, tube-bearing crinoid, *Batocrinus*. Sub-

sequently, the drilling interpretation was corroborated by reports of drilled blastoids known to have been infested by platyceratids (Baumiller, 1993a, 1996; Baumiller and Macurda, 1995). By accessing the pelmatozoan calyx through a drill-hole rather than through the anal opening makes strict platyceratid coprophagy unlikely; rather, the drilling allowed these gastropods access to the viscera housed in the calyx.

Although the above observations argue for a detrimental effect on crinoids by the associated platyceratids, was the interaction predatory or parasitic? Evidence of drilling may be interpreted as indicating predation based on the way in which it is employed by most drilling gastropods, such as the naticids and muricids. However, several lines of evidence argue against drilling by platyceratids being predatory, including (1) instances of two drillholes on some crinoid and blastoid specimens, (2) instances of scars around drillholes, (3) presence of healed drillholes, and (4) examples of platyceratids found in place over drillholes. The latter association supports a long-term parasitic interaction because of the higher probability of catching a parasite, rather than a predator, 'in the act'. Finally, it is worth noting that kleptoparasitism is a strategy employed by some modern gastropods, most notably members of the Capulidae, some of which drill their molluscan hosts and feed on food collected by their host.

The hypothesis that platyceratids were coprophagous, gametophagous or parasitic on pelmatozoan echinoderms predicts that nutrients captured by their hosts would have to be sufficient to satisfy the energetic needs of both organisms. This prediction can be evaluated quantitatively by estimating the rates of nutrient capture of host crinoids and the energetic requirements of the host crinoid and infesting parasite. I will employ this approach below by using morphological data from fossil crinoids and platyceratids, physiological data from modern crinoids and gastropods, and crinoid nutrient capture rates based on quantitative filtration models. The following questions will be addressed: (1) is the parasitic/coprophagous/gametophagous interpretation energetically feasible, i.e. did crinoids capture sufficient nutrients to supply their needs and those of the in-

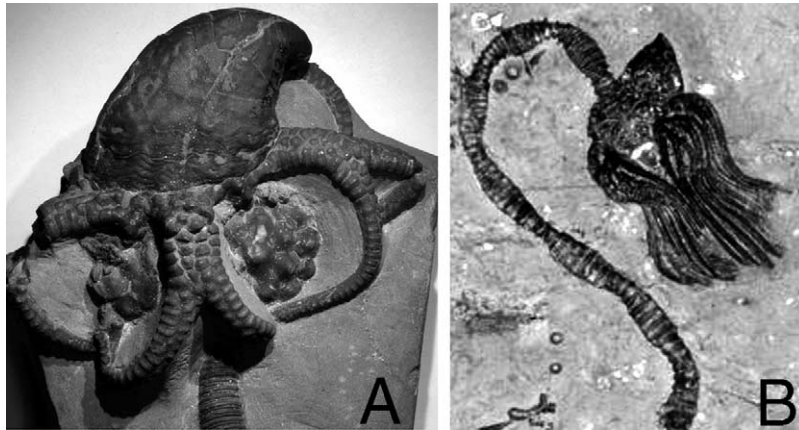


Fig. 1. Examples of Mississippian platyceratids attached crinoids. A: A platyceratid on *Gilbertsocrinus*. B: A platyceratid on *Platytrinites*.

festing platyceratid?, (2) could cost–benefit explain the preferences of platyceratids for crinoids with dense filters (pinnulate arms)?, 3) how does cost–benefit analysis of parasitism/coprophagy on crinoids compare to that of predation?

2. Materials and methods

2.1. Parasite–host interactions

The reconstruction of biotic interactions in the fossil record is extremely difficult. Even when direct evidence of an interaction is preserved, as in the platyceratid–crinoid case, the grossest details of the interaction still remain obscure. Therefore, any approach that provides additional insights should be explored, and this was the rationale behind extending the cost–benefit approach to crinoids and platyceratids. The cost–benefit approach used here relies on analogies from modern systems that may, or may not be strictly applicable. But such actualistic approaches must serve as the initial null-model, and, not surprisingly, they continue to be widely used.

The approach taken here makes one fundamental assumption: it assumes that over physiologically relevant time scales, an organism must be at an energetic equilibrium, with energy intake equal to energy expended. In a parasite–host relationship, the energy taken in by the host is in the form

of captured nutrients. This energy must supply the energy needs of both the host and the parasite and it consists of expenditures associated with maintenance, growth, and reproduction of both organisms.

Subsidiary assumptions, however, are plentiful and involve the choice of appropriate parameters for estimating the energy captured by the crinoid and the metabolic needs of the crinoid and gastropod. For most of these, modern analogs had to be used and, as is the case with most uniformitarian assumptions, there are arguments for, as well as against, any given analog. Below I describe and justify some of my choices.

2.1.1. Energy captured by crinoid as host

Assuming a host–parasite or host–coprophage interaction between crinoids and platyceratids, all the captured energy would be in the form of particulate nutrients collected by the crinoid. As passive suspension feeders, crinoids capture particulates using a planar filter formed by the radially extended arms lined with microscopic tube feet. As particle-laden water currents move through the filter, some of the particles are intercepted by the tube feet. These particles are then transferred into a food groove that lines each of the arms, and from there they are moved via ciliary currents and, other tube feet, to a centrally located mouth.

The rate of particle capture is governed by the

Table 1
Morphology of crinoid tube feet

Variable	Value (m)	Reference
Tube foot diam (DF)	1.00E-04	Meyer, 1979, Holland et al., 1986
Tube foot gap pinnulates	9.00E-05	Brower, 1994
Tube foot spacing = gap+DF (H1) pinnulates	1.90E-04	
Tube foot gap non-pinnulates	1.60E-04	Brower, 1994
Tube foot spacing = gap+DF (H1) non-pinnulates	2.50E-04	

Table 2
Scaling relationship of pinnulate crinoids

Dependent variable	Independent variable	Intercept	Exponent	Reference
Cup height (mm)	size	0.784	1.25	Brower, 1994
Branch spacing (mm) (H2)	crown volume	2.48	−0.295	Brower, 1994
Cup+tegmen volume (mm ³)	size	0.873	3.07	Brower, 1994
Filter area (mm ²)	crown volume	31.5	0.679	Brower, 1994
Crown volume (mm ³)	size	1.69	4.01	Brower, 1994
Plate thickness (mm)	cup height	0.4	0.89	Brower, 1996

size and geometry of the filter and filter fibers, the velocity of the current, the size, density and concentration of particles, and viscosity and density of the fluid. In this study, the size and geometry of the filter and filter fibers were obtained from the morphology of fossil and extant crinoids (Table 1 and 2). Since detailed data for crinoids are available only for a few taxa, the approach used here was to find the closest morphological analog to crinoids known to have been infested by platyceratids. Most platyceratid–crinoid associations involve camerate crinoids, a group characterized by arms with very fine branches, called pinnules. Brower (1994) provided detailed morphometric data for a camerate crinoid, and these were used as a baseline in this study.

The size distribution and concentration of particulate nutrients were assumed to correspond to those found in modern marine settings (Table 3), and viscosity and density of the fluid were those

of sea water at 25°C (Table 4). Given values for the above variables, particle capture rates, and corresponding energy capture rates, were calculated for a range of current velocities using previously developed, and empirically tested, analytical solutions (Baumiller, 1993b; Fig. 2). The energetic content of the particles was based on published data on modern marine settings (Table 3). Not all of the caloric energy present in the captured nutrients is converted to metabolic energy: the organism assimilates only some portion of this energy (Table 5).

2.1.2. Energy costs of parasitism

In a parasite–host relationship, the energetic needs of both organisms must be considered. The metabolic costs of the host crinoid were estimated using data for metabolic rates of modern crinoids. These estimates do not differentiate between costs associated with growth, maintenance

Table 3
Properties of particles

Variable	Value	Reference
Particle concentrations	0.1 (ml oxygen/l)	Gardner et al., 2000
Min size (Dpmin)	1.00E-05 m	Hung et al., 2000
Max size (Dpmax)	2.00E-04 m	Sharp, 1973

Table 4
Properties of the fluid (sea water)

Variable	Value	Reference
Current velocity	2–30 cm/s	
Viscosity	1.00E-03 Pa s	Vogel, 1994
Density	1000 kg/m ³	Vogel, 1994

and reproduction. Moreover, the relationship between standard metabolic rate and mass is non-linear, and is commonly expressed in the form of an allometric equation:

$$\text{SMR} = aW^b \quad (1)$$

where SMR is the standard metabolic rate (watts), W is the mass (in kg), and the values of a and b are empirically derived (Table 5). To calculate the rate of metabolic energy expenditure of a fossil crinoid host, values of a and b for modern crinoids were used in the equation with an estimated mass of the crinoid. The latter value was based on volume estimates of the fossil and data on modern crinoid skeletal densities.

The energy needs of an infesting platyceratid can also be estimated using metabolic rates of modern snails. The physiology and behavior of the predatory snail, *Polinices*, have been extensively studied and although *Polinices* is phylogenetically distant and ecologically distinct from the platyceratids, it is unlikely that this makes it any less suitable as a model than any other modern gastropod, with the possible exception of *Capulus* for which, unfortunately, there are no data. *Polinices* was therefore used as the model here. I converted data from Edwards and Huebner (1977) on ingestion rates in *Polinices* to find an expression for metabolic rate:

$$\text{maximum metabolic rate (watts)} = 2 \times 10^{-8} \text{ Size (mm)}^{3.6} \quad (2)$$

The more general expression for poikilotherms (Peters, 1983) was also used:

$$\text{SMR (watts)} = 0.14 \text{ W (kg)}^{0.751} \quad (3)$$

To use Eq. 3, a relationship between size and mass is needed and here this was based on extant *Polinices* (Kitchell et al., 1981).

2.2. Predator–prey interactions

In evaluating the cost–benefit of platyceratid–crinoid association in terms of a predator–prey interaction, it is assumed that a predatory platyceratid would consume the edible tissues housed in the crinoid calyx and that the energetic costs of predation would include capture, handling, and digestion.

2.2.1. Energy available from crinoid as prey

Since modern crinoids lack a distinct, subspherical calyx, an estimate of this value comes from the scaling of edible soft tissues in the echinoid, *Tripneustes* (figure 7 in Hughes and Hughes, 1981; Table 5). Using this relationship, the energetic content of the crinoid cup can be approximated as a function of crinoid size. Since Paleozoic crinoid eggs and gonads were likely held within the body cavity whereas they are found on the pinnules of extant crinoids (Lane, 1984), using the echinoid as a model seems appropriate.

2.2.2. Energy costs of predation

The costs involved in predation include all energy expended in search, capture, handling, and digestion of the prey. In estimating the cost–benefit of predation, data on modern predatory snails

Table 5
Physical and physiological properties used for crinoids

Variable	Value	References
Density of skeletal mass (g/cm ³)		
range	1.2–1.7	Brower, 1987; Baumiller, 1992
value used	1.3	
Assimilation	15%	Fox, 1936; Schroeder, 1981; Peters, 1983.
Dry tissue as % total mass	15	McClintock et al., 1990
Edible organic tissue in cup (g)	cup height ³ /148 (cm)	Hughes and Hughes, 1981
Energy content of dry tissue (kJ/g)	3	McClintock et al., 1990
SMR (w/g)	8–40 × 10 ⁵	Baumiller and LaBarbera, 1989
SMR = aW^b	$a = 0.14$; $b = 0.751$	Peters, 1983

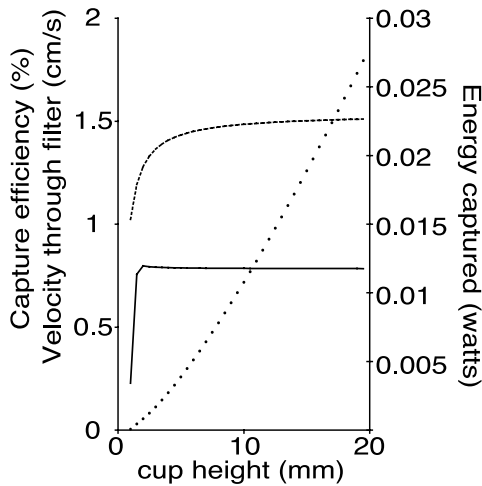


Fig. 2. Particle capture efficiency (solid line), current velocity through the crinoid filter (dashed line), and total energy/time (dotted line) captured by a crinoid as a function of its size at an ambient current velocity of 10 cm/s. The crinoid morphology is modeled on a Paleozoic pinnulate (Tables 1 and 2).

were used. Hughes and Hughes (1981) reported data on the handling time of cassid gastropods preying on sea urchins. In their study, handling time varied as a function of sea urchin size:

Handling time (minutes) =

$$15.5 \times \text{Tripneustes diameter (cm)} + 45.3 \quad (4)$$

Cassids preying on *Tripneustes* served as one model for platyceratids preying on crinoids, but because cassids are much larger than platyceratids and because the test of *Tripneustes* is much thinner than that of crinoids, another estimate of handling time was employed. This estimate was based on the data on *Polinices* and its molluscan prey (Kitchell et al., 1981). The rate reported by Kitchell et al. (1981), 0.0223 mm/h, was independent of predator size. The cassid–*Tripneustes* data provided a higher estimate of drilling rate than the *Polinices* data, probably because the stereomic structure of the echinoderm skeleton is much different from that of molluscan skeleton. In both instances, the energy expenditure of the predatory platyceratid was calculated as the product of the handling time and its SMR (Eq. 3).

3. Results

3.1. Energetic feasibility of parasitic/coprophagous platyceratid

As Fig. 3 illustrates, the energy captured by pinnulate crinoids ranging in size from 1 to 20 mm (cup height) exceeded their SMRs in a 10-cm/s current and under normal particle concentrations of sea water. The difference between energy capture and energy expenditure could be either used in other activities (maintenance, reproduction, etc.) or might provide nutrients for an infesting platyceratid. Using data on metabolic rates of modern gastropods as an analog for platyceratid rates (Eqs. 2 and 3) and the relationship between size and mass in *Polinices* (Kitchell et al., 1981), the maximum size of an infesting platyceratid that could be supported by this energy was calculated. The results (Fig. 4) show that even small pinnulate crinoid feeding in a 10-cm/s current could capture sufficient nutrients to satisfy the metabolic needs of moderately large platyceratids, often larger than the height of the crinoid cup. This seemingly implausible result is consis-

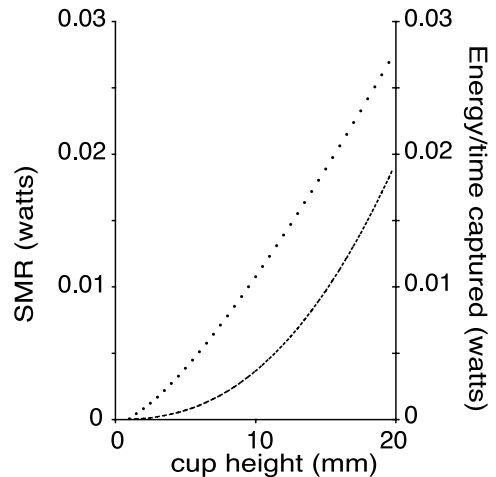


Fig. 3. Total energy/time (dotted line) captured by a crinoid and the energy expenditures, expressed as SMR (dashed line), as a function of its size at an ambient current velocity of 10 cm/s (energy captured same as in Fig. 2). The crinoid morphology is modeled on a Paleozoic pinnulate (Tables 1 and 2).

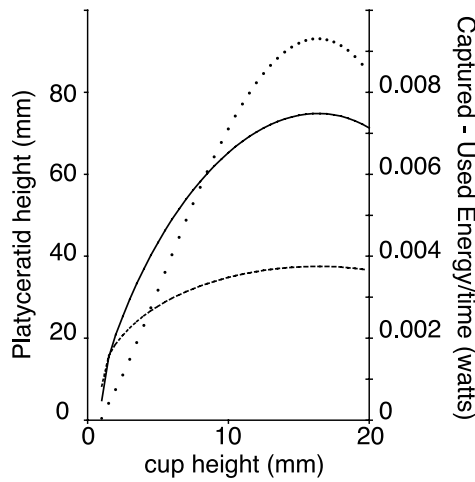


Fig. 4. Surplus of energy/time captured by a crinoid as a function of its size at an ambient current velocity of 10 cm/s (dotted line) and the maximum size of platyceratids that could infest them. Solid line: maximum platyceratid size estimate using Eq. 2; dashed line: maximum platyceratid size using Eq. 3. The crinoid morphology is modeled on a Paleozoic pinnulate (Tables 1 and 2).

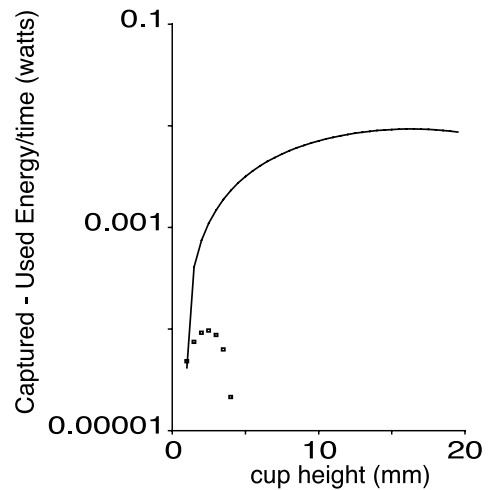


Fig. 5. Surplus of energy/time captured by a pinnulate crinoid (solid line) and a non-pinnulate crinoid (squares) as a function of its size at an ambient current velocity of 10 cm/s. Pinnulate crinoid morphology is modeled on a Paleozoic pinnulate (Tables 1 and 2), that of a non-pinnulate crinoid is modeled on a Paleozoic non-pinnulate (Table 6).

tent with fossil specimens (Fig. 1) sometimes showing large snails on small crinoids.

3.2. Selectivity of host crinoids by platyceratids

The fossil record of platyceratid infestation is dominated by examples of pinnulate, camerate,

and advanced cladid crinoids. A tabulation of infested genera through the Phanerozoic shows that 42 are pinnulate and five non-pinnulate. Even accounting for the greater number of described pinnulate genera during the Paleozoic (515 pinnulates and 324 non-pinnulates, Sepkoski's unpublished generic compendium), the selectivity is significant at $P < 0.0001$ using a Chi-squared test. It might

Table 6
Scaling relationship of non-pinnulate crinoids

Dependent variable	Independent variable	Intercept	Exponent	Reference
Branch spacing (mm) (H2)	crown volume	0.308	-0.471	Brower, 1992
Cup+tegmen volume (mm ³)	cup height	0.201	3.35	Brower, 1992
Filter area (mm ²)	crown volume	20.1	0.749	Brower, 1992
Crown volume (mm ³)	cup height	1.22	3.59	Brower, 1992
Plate thickness (mm)	cup height	0.4	0.89	Brower, 1996

Table 7
Parameters used in estimating drilling costs of crinoid cup of the form: dependent variable = m (independent variable) + B

Dependent variable	Independent variable	Intercept B	Slope m	Reference
Handling time (min)	Cup height (cm)	45	15.5	Hughes and Hughes, 1981
Handling time (h)	Plate thickness	0	0.5	Kitchell et al., 1981
Filter area (mm ²)	Crown volume	20.1	0.749	Brower, 1992
Crown volume (mm ³)	Cup height	1.22	3.59	Brower, 1992

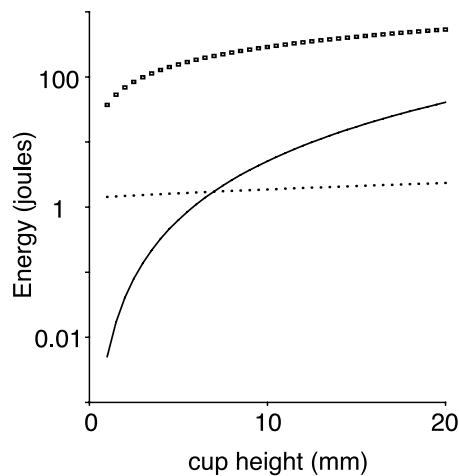


Fig. 6. Energetics of predator–prey relationship between a 20-mm-high platyceratid and pinnulate crinoid. The energy content of crinoid calyx soft tissues available to predator (solid line). The energetic costs of predation based on a *Polinices*–mollusk model (squares) and a cassid–*Tripneustes* model (dotted line) as a function of crinoid size. Pinnulate crinoid morphology is modeled on a Paleozoic pinnulate (Tables 1 and 2).

appear obvious that crinoids with pinnulate arms (dense filters) should capture more nutrients and thus serve as better hosts to infesting platycerata. But because these arms are typically more massive, the metabolic needs of such crinoids would also be greater, and so it is important to quantitatively assess the available excess energy (captured–used). To do so, one needs to apply the approach developed above to a non-pinnulate crinoid. Again, Brower (1992) provided detailed morphometric data for a non-pinnulate Paleozoic crinoid and these data were used for comparison (Tables 6 and 7, Fig. 5).

As Fig. 5 illustrates, pinnulate crinoids show a vastly greater excess of energy than do non-pinnulates (note logarithmic scale). One can further ask whether the excess energy captured by non-pinnulate crinoids could support platyceratid metabolism.

3.3. Cost–benefit of parasitism/coprophygy vs. predation

Finally, it is possible to ask whether crinoids would have provided a better source of nutrients

for snails employing a parasitic or a predatory strategy. The cost–benefit of parasitism was explored above, and those associated with predation were approached similarly (Table 7). Fig. 7 illustrates the energy gained by a predatory snail, 20 mm in height consuming the soft tissue within a crinoid calyx. The energetic costs associated with this strategy were those involved in spending time in searching, drilling, and consuming the prey while operating at a SMR. These costs were estimated based on the same two modern analogs: a cassid preying on the sea urchin, *Tripneustes*, and a *Polinices* preying on mollusks (Table 7). The results indicate that applying the latter model leads to energetic costs of predation being greater than its gains (Fig. 6). Assuming the cassid–*Tripneustes* model, the line representing the energy gained from ingesting the crinoid crosses the line representing the cost of predation at a crinoid size of 7 mm, i.e. crinoids larger than that size would provide sufficient nutrition to overcome the costs

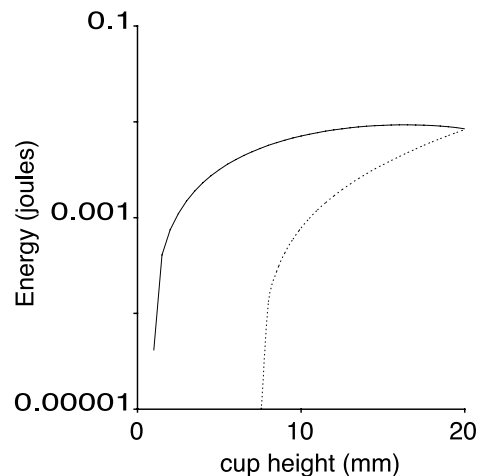


Fig. 7. Comparison of energetics of predator–prey and parasite–host relationship. The solid line represents the net energetic gain/time for a 20-mm snail infesting a pinnulate crinoid in a 10-cm/s current. The dashed line represents the net energy gain of a 20-mm predatory snail based on a cassid–*Tripneustes* model. Note that a predatory relationship is energetically feasible only when crinoids are larger than 8 mm (cup height); a predator–prey relationship modeled on a *Polinices*–mollusk relationship is not feasible energetically with costs exceeding gains for the entire range of crinoid sizes. Pinnulate crinoid morphology is modeled on a Paleozoic pinnulate (Tables 1 and 2).

of predation. We can compare these gains to those of a parasitic snail of the same size infesting crinoids (Fig. 7). In Fig. 7, the net energy gains were normalized to time, such that the parasitic and predatory energetics are expressed in units of power. Note that in the 1–20-mm crinoid cup size range, the gains of parasitism exceed those of predation, though they converge at the larger crinoid sizes and the relationship would reverse above 20-mm cup height.

4. Conclusions

There is broad consensus that the platyceratid–crinoid relationship represented either coprophagy (neutral to host) or parasitism/gametophagy (detrimental to host), and from a cost–benefit perspective those two strategies are nearly indistinguishable – the net energy captured by the crinoid must satisfy both organisms. Cost–benefit analyses were used here to quantitatively explore whether crinoids known to have been infested by platyceratids were capable of capturing sufficient nutrients for them and the infesting gastropod, making the parasite/coprophage interpretation feasible. The known selectivity of platyceratids for crinoids that had large, dense filters, i.e. those that were pinnulate, also finds support in the calculations: non-pinnulate crinoids would have made much poorer suppliers of nutrients. This result is not an obvious consequence of the filtration model because there are trade-offs between dense filters and capture rates (see Baumiller, 1993b). Also, even though pinnulate crinoid filters have greater particle capture rates under most conditions, their larger size also makes their energy consumption greater, and it is the difference between what is captured and what is consumed that would matter to a parasitic snail.

Finally, the cost–benefit approach leads to an interesting result when comparing parasitic and predatory strategies. Based on cost–benefit alone, it appears that crinoids were better hosts than prey for gastropods. This result should not be so surprising: crinoids are capable of capturing particulate nutrients at high rates but, like other echinoderms, possess little soft tissues that are

typically interspersed as stroma within the stereom microstructure. Even today's crinoids do not appear to be a major food item of any predators, although they may be subject to some predation pressure (Meyer, 1985; Oji, 1996, McClintock et al., 1998). Platyceratids were clearly capable of drilling their pelmatozoan hosts (Baumiller, 1990) and thus could overcome skeletal defenses. Yet, there is no evidence at present to suggest that the drilling abilities of platyceratids were ever exploited for predation. This may, of course, reflect some other constraint that prevented them from shifting to a predatory strategy, for example, because their drilling abilities were limited. However, as this analysis shows, even if they were as capable as modern snails in capturing and consuming their prey, they would have received a greater energetic return from infesting pinnulate crinoids. It is thus possible that the nature of the relationship was a consequence of optimal foraging rather than some intrinsic constraints (see Leighton, 2002 for a discussion of assumptions and limitations of optimal foraging).

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