FOSSIL RECORD OF PARASITISM ON MARINE INVERTEBRATES WITH SPECIAL EMPHASIS ON THE PLATYCERATID-CRINOID INTERACTION

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ABSTRACT—The paleontological literature on marine invertebrates is rich in supposed examples of parasitism and our tabulation shows a nearly even distribution of reported cases through the post-Cambrian Phanerozoic. Slightly lower frequencies characterize the Triassic and Jurassic and higher frequencies the Cretaceous and Tertiary, and the pattern roughly mirrors Sepkoski's (1984) marine diversity curve. The total number of parasitic associations for any geologic period rarely exceeds a dozen, yet few of the reported examples provide explicit criteria distinguishing parasitism from predation, commensalism, or mutualism. We evaluated the published examples using the following criteria: (1) evidence of a long-term relationship between two organisms, (2) benefit of interaction to supposed parasite, and (3) detriment of interaction to the host. We found that only in exceptional cases were these criteria fulfilled. One example that provides much information on parasitic interactions involves platyceratids and crinoids and we summarize the evidence for the parasitic interaction between these two groups of organisms.

INTRODUCTION

BIOTIC INTERACTIONS can be represented in terms of the ecological and/or evolutionary consequences that they have on the interacting organisms. From an ecological perspective, interactions may be considered to be positive (+), neutral (0), or negative (-). In the case of two interacting organisms, there exist six possible combinations: amensalism (0,-), competition (-,-), mutualism (+,+), commensalism (+,0), exploitation (+,-), and toleration (0,0) (Clarke, 1954). Two types of exploitative behavior are recognized: predation and parasitism. Both are interesting ecologically and evolutionarily because they may lead to reciprocal evolution, or an "arms race," between predator and prey, or host and parasite. However, the difference between parasitism and predation is one of degree rather than kind. One difference is that while predators typically kill their prey, parasites *might* kill their hosts, but not without first making use of their living victims for an extended period. As a first step in recognizing parasitism it is therefore necessary, though not sufficient, to establish that an association involved a long-term relationship between two organisms. It must further be demonstrated that the interaction benefited the infester and was detrimental to the host. It is understood that we must know the identity of the host, and, if we are to explicitly demonstrate the benefit of the interaction to the parasite, we should know its identity as well. Not surprisingly, for paleontologists, "...recognition of a fossil association as being parasitic may not be easy" (Conway Morris, 1981, p. 491).

FOSSIL RECORD OF PARASITES ON MARINE INVERTEBRATES: A SURVEY

Methods.—We reviewed the literature to explore the fossil record of parasites on marine invertebrates. We were interested not only in discerning temporal patterns of inferred parasitism, but in the type and quality of data that were used to establish the nature of the relationship. Our list may not be exhaustive, but it should not be biased in any systematic way. In collecting the data we relied

TABLE 1—Fossil record of parasites on marine invertebrates.

Host	Parasite	Category	Parasite benefit	Host detriment	Evidence for duration of relationship	First occurrence	Last occurrence	References
arthropod	fungi	3	nutrients	?	fungal mass in coprolites	Silurian	Tertiary	Taylor & Osborn, 1996
belemnite	acrothoracid barnacle	3	?	?	teardrop-shaped boring	Jurassic	E. Cretaceous	Seilacher, 1968
bivalve	capulid gastropod	1	?	?	attachment, scars, borings	L. Cretaceous	Tertiary	Hayami & Kanie, 1980
bivalve	cestode or trematode	3	?	?	pearls	Triassic	Tertiary	Herdman, 1906
bivalve	Clionid sponge	3	?	?	borings	Cretaceous	Tertiary	Barry et al., 1972
bivalve	polychaete or sipunculid	2	?	?	tube-like borings	Tertiary	Tertiary	Savazzi, 1995
bivalve (venerid)	trematode	3	?	?	pits	Tertiary (Miocene)	Tertiary	Boucot, 1990
blastoid	platyceratid gastropod	1	nutrients	nutrients	attached, scars, borings	Devonian	Mississippian	Baumiller, 1996
brachiopod	acrothoracid barnacle	2	?	?	elongate borings	L. Devonian	Pennsylvanian	Rodriguez & Gutschick, 1977
brachiopod	polychaete or gastropod	3	?	?	borings	M. Ordovician	Tertiary	Baumiller et al., 1999; Leighton, 2001
brachiopod	uncertain	3	?	?	tube secretions	Devonian	Devonian	MacKinnon & Biernat, 1970; Chatterton, 1975
brachiopod	uncertain	3	?	?	calcareous partitions	L. Silurian	L. Silurian	Boucot & McCutcheon, 1986
bryozoan	algae and fungi	3	?	?	microstructure	Ordovician	Tertiary	Elias, 1966
bryozoan	hydroid/ colonian ascidian	3	?	?	embedment structures	Late Ordovician	Late Ordovician	Palmer & Wilson, 1988
bryozoan	serpulid polychaete	3	?	?	tube secretions	Upper Cretaceous	U. Cretaceous	Ehrhard Voight, 1955
chitinozoa	bacteria and fungi	3	?	?	borings	Ordovician	Mississippian	Grahn, 1981; Sutherland, 1994
conularid	uncertain	3	?	?	pearls	Pennsylvanian	Pennsylvanian	Babcock, 1990
crinoid	myzostomid annelid	2	?	?	galls, pits	Ordovician	Tertiary	Welch, 1976; Brett, 1978
crinoid	platyceratid gastropod	1	nutrients	nutrients	attached, scars, borings	M. Ordovician	Permian	Rollins & Brezinski, 1988
crinoid	uncertain	3	?	?	circular pits	M. Ordovician	Permian	Brett, 1985
cystoid	platyceratid gastropod	1	nutrients	nutrients	attached, scars, borings	M. Silurian	M. Silurian	Boucot, 1990
decapod	bopyrid isopod	2	nutrients	soft tissues	carapace deformation	L. Jurassic	Tertiary	Glaessner, 1969
decapod	rhizocephalan	2	nutrients	sex organs	claw feminization/castration	L. Jurassic?	Tertiary	Boucot, 1990
echinoid	barnacle	2	?	?	elongate borings	L. Cretaceous	Tertiary	Madsen & Wolff, 1965; Marouf, 1999
echinoid	copepod	2	?	?	internal galls	Jurassic	Tertiary	Solovjev, 1961; Mercier, 1937; Marouf, 1999
echinoid	eumelid gastropod	2	nutrients	soft tissues	borings	Cretaceous	Tertiary	Kier, 1981; Alekseev & Endelman, 1989
echinoid	gastropod	1	?	?	deformed spines	Cretaceous	Tertiary	Tasnádi-Kubacska, 1962
echinoid	myzostomid annelid	2	?	?	galls	Tertiary (Miocene)	Tertiary	Roman, 1952
echinoid	prosobranch gastropod	2	?	?	skeletal malformations	E. Cretaceous	Tertiary	Boucot, 1990
gastropod (platyceratid)	acrothoracid barnacle	2	?	?	elongate borings	E. Devonian	Pennsylvanian	Baird et al, 1990
graptolite	uncertain	3	?	?	closed blisters	E. Ordovician	L. Silurian	Bates and Loydell, 2000
graptolite	uncertain	3	?	?	open-ended tubes	E. Ordovician	L. Silurian	Bates and Loydell, 2000
graptolite	uncertain	3	?	?	tubothecae	E. Ordovician	E. Ordovician	Conway Morris, 1981

heavily on two important reviews of parasitism: Conway Morris' (1981) "Parasites and the fossil record," and Boucot's (1990) "Evolutionary paleobiology of behavior and coevolution."

We evaluated the published examples in terms of several criteria (Table 1). In considering the identity of the parasite, if the inferred parasite was directly observable in association with the host, it was assigned to "category 1." If the identity of the parasite was inferred from a well-constrained proxy, namely the trace fossil that it produced, we assigned it to "category 2." In all other instances, the identity of the parasite was considered more speculative and assigned to "category 3."

We also considered the evidence presented for the benefit that was gained by the parasite and for the detrimental effects on the host. Finally, data used to infer a long-term duration of the association were noted.

Results.—Our search produced a substantial number of inferred cases of parasitism (Table 1), and, as Figure 1 illustrates, reports of parasitic association are quite evenly distributed through the post-Cambrian Phanerozoic. Although slightly lower frequencies characterize the Triassic and Jurassic and higher frequencies the Cretaceous and Tertiary, the coarse temporal and taxonomic resolution prevents us from assigning much significance to these differences, though it is worth noting that the pattern roughly mirrors Sepkoski's (1984) marine diversity curve. The total number of parasitic associations for any geologic period rarely exceeds a dozen, and if we consider those associations for which the identity of the parasite is well-constrained, based on co-occurrence or characteristic trace fossils (categories 1 and 2 in Fig. 1), the number is lower still.

To illustrate our scheme, we consider the bivalve-capulid gastropod association reported by Hayami and Kanie (1980). These authors reported specimens of Cretaceous capulid gastropods attached to the valves of inoceramids. Since the identity of the interacting organisms is known, this represents "category 1" in our scheme. Hayami and Kanie (1980) inferred that this interaction represented parasitism because it was ecologically long-lived, as evidenced by the presence of attached specimens, and was analogous to the modern capulids that are found in association with bivalves, gastropods, brachiopods, and annelids. Extant capulids are suspension feeders and can be facultative semi-parasites or parasites: they can

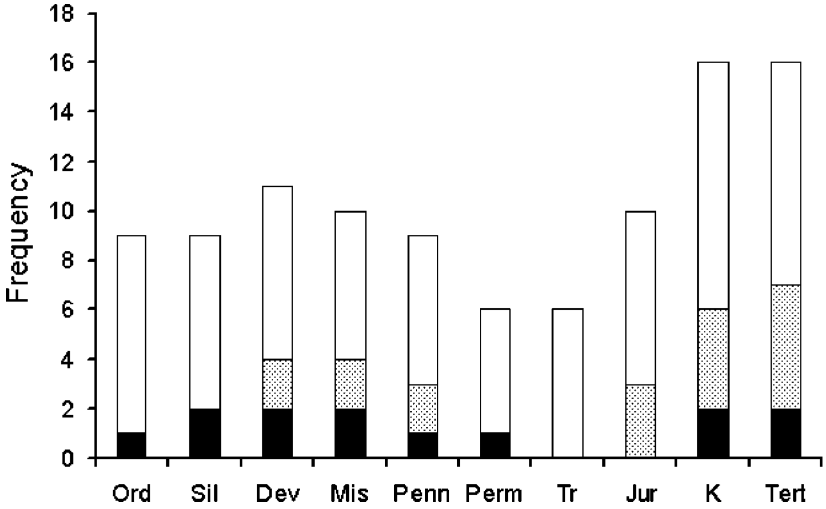

FIGURE 1—Temporal distribution of reported parasites on marine invertebrates. Black, stippled, and white bars represent categories 1, 2, and 3, respectively. Categories 1, 2, and 3 explained in text. (Data from Table 1.)

feed from the inhalant current created by the ciliary activity of the host (Thorson, 1965), or by using their pseudoproboscis to divert particles captured by the host to its own mouth (Pernet and Kohn, 1998). Thus, in our scheme, "nutrients" benefit the parasite, and their loss is a detriment to the host.

As Table 1 indicates, examples of parasitism such as the bivalve-capulid association, where the identity of the interacting organisms and the nature of the benefit/detriment can be reliably assessed, are rare in the fossil record. Most common are instances where a trace fossil, or a growth abnormality, is interpreted as having been parasite-induced, where the identity of the parasite cannot be ascertained, and where the beneficial effects on the parasite and the detrimental effects on the host are poorly constrained. The case of the Pliocene bivalve, *Isognomon*, serves as an illustration of such parasitic interpretations. Savazzi (1995) reported seven different types of anomalies in the hinge region of 14 of 24 specimens of *Isognomon maxillatus* from the Upper Pliocene of Italy. The size and shape of some of the cavities suggested that they were produced by a worm-like organism. According to Savazzi (1995, p. 136), "…a polychaete could be a reasonable candidate," and a "…sipunculid could also be a possible candidate." However, because the observed teratologies, or malformations, find no exact modern analogs, we categorize the identity of the parasite as "inferred" (category 3).

The *Isognomon* example also illustrates the problems in assessing the benefit of an association to the parasite and its detrimental effects on the host. The benefit to the infesting organism may seem obvious because the host is at least providing the infester with a suitable life position or protection, but unless the infester's effect on the host can be shown to be detrimental, such an interaction could represent mutualism or commensalism. For *Isognomon,* Savazzi (1995, p. 137) chose parasitism, which he claimed was "much more likely," because the position of some of the anomalies would have made it difficult for the infesting organism to access sea water directly while allowing it to tap into the digestive system or the hemocoele of the bivalve. In our scheme, we leave the question of benefit/detriment for *Isognomon* as undetermined ("?"), in part because Savazzi (1995) did not specify whether it involved nutrients, tissues, or something else that was benefiting the parasite and causing harm to the host. Although one might infer that the parasite was stealing nutrients from the host, we considered those fossil examples for which no modern analog for parasitism had been presented, and no explicit test was used to reject commensalism or mutualism, as "undetermined."

In our classification scheme, the vast majority of inferred cases of parasitism are "undetermined" with regard to benefit/detriment (Table 1). In general, the inference of parasitism in these cases is based on accepting "reaction" features as detrimental to the host. Reaction features, such as pearls, galls, blisters, and deformations, do indicate that the host responded biotically to the infester, but whether such a response placed the infested individual at a selective disadvantage relative to uninfested conspecifics has rarely been explored. Of course, it is plausible to assume that the energetic costs associated with the "reaction" may place infested individuals at some disadvantage, but such costs may be quantitatively, and thus selectively, trivial. Thus, even the swollen, distorted, and excavated stems of crinoids caused by the reaction to some infester that have been claimed as cases of "true parasitism" (Pickett, 1973, p. 342), remain enigmatic and may be more appropriately treated as commensal (Franzen, 1974; Brett, 1978, 1985; Baird et al., 1990).

Many of the examples in Table 1 illustrate the problems faced by paleontologists in distinguishing between parasitism, commensalism, and mutualism—problems that have long been recognized (Conway Morris, 1981; Savazzi, 1995). Distinguishing between predation and parasitism can prove equally difficult. Complete boreholes in the tests of fossil organisms have generally been interpreted as predatory, especially when morphologically similar holes are produced by extant predators, such as muricid or naticid gastropods. However, when such boreholes precede the known first appearance of modern predatory drilling gastropods, and the causative organism cannot be determined, their interpretation has been less certain. This has been especially true for boreholes in Paleozoic invertebrates (Fisher, 1962; Carriker and Yochelson 1968; Sohl, 1969). For many of these boreholes, parasitism has been considered a plausible hypothesis (Buehler, 1969; Ausich and Gurrola, 1979; Conway Morris and Bengtson, 1994). A parasitic interpretation of complete Paleozoic boreholes has become even more tenable after it was shown that platyceratid gastropods were capable of drilling echinoderms (Baumiller, 1990, see below), and Table 1 includes several examples of inferred parasitism by platyceratid gastropods. The long range of platyceratids (Ordovician to Permian), their abundance, occurrence in a broad range of marine settings, known association with a variety of taxa (crinoids, blastoids, cystoids), and sedentary nature implies that they should be considered as the "null-hypothesis" when seeking the culprit of complete Paleozoic boreholes, such as those in brachiopods (Baumiller et al., 1999; Kowalewski et al., 2000; Leighton, 2001). Given the abundance and range of platyceratids, newly published and yet unpublished data relevant to their life habit, and the fact that they are our favorite example, we will present a review of the data and their status as parasites.

PLATYCERATIDS AND CRINOIDS

Record of interaction.—One of the classic examples of biotic interactions in the fossil record is that between platyceratid gastropods and crinoids (Fig. 2). The consistent occurrence of platyceratid gastropods preserved attached to the calyxes of crinoids was noted by mid-nineteenth century

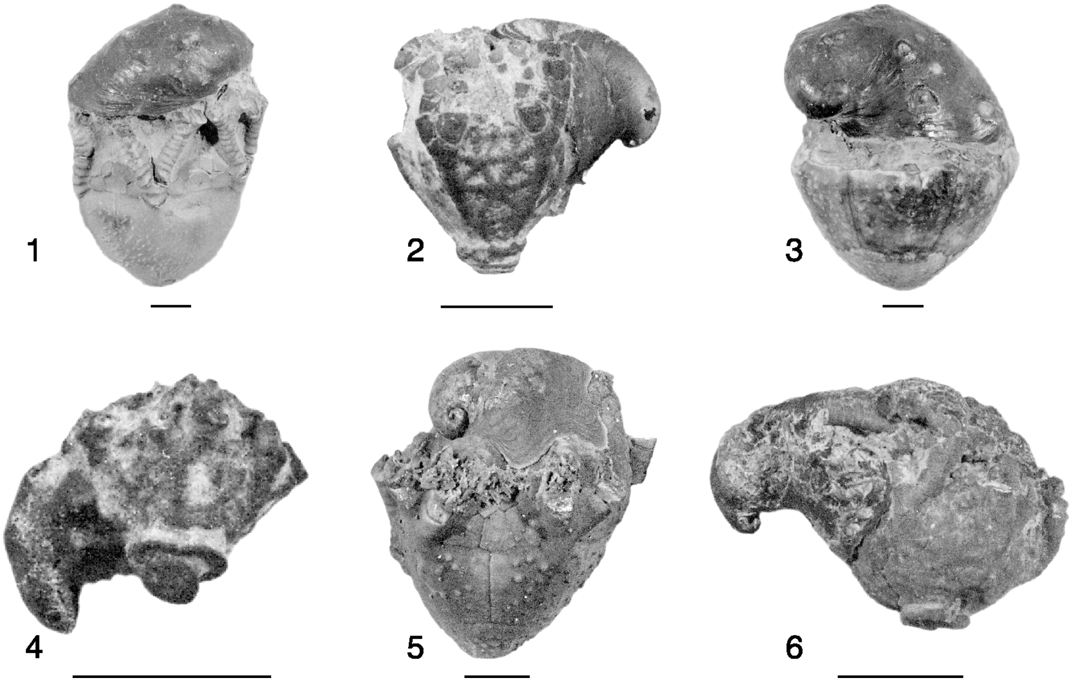

FIGURE 2—Examples of platyceratid-crinoid association. All specimens from Middle Devonian strata. Scale bar = 0.5 cm. 1, 3, *Arthroacantha carpenteri*, UMMP 23915, Arkona Shale, Thedford, Ontario. 2, *Corocrinus calypso*, UMMP 24170, Arkona Shale, Arkona, Ontario. 4, *Gennaeocrinus variabilis*, 224G, S. Virgilis personal collection, Bell Shale, Rockport, Michigan. 5, *Arthroacantha carpenteri*, K. Dobson personal collection, Silica Shale, Sylvania Ohio. 6, *Corocrinus calypso*, UMMP 57528, Arkona Shale, Hungry Hollow, Ontario.

paleontologists (Austin and Austin, 1843; Yandell and Shumard, 1847; Owen, 1862; Meek and Worthen, 1866). The record of this association extends from the Ordovician to the Permian (Fig. 3), and not only is the identity of the interacting organisms known, but already these early workers had recognized that the gastropods and crinoids must have been interacting during life. However, establishing the nature of that interaction proved a more elusive goal.

Nature of interaction.—One of the earliest interpretations of the gastropod-crinoid fossils was that of Austin and Austin (1843), who assumed that the specimens represented crinoids caught in the act of feeding on gastropods. The predator-prey interpretation was rejected by Meek and Worthen (1866, 1868), who noted that the irregular shape of the gastropod margin forming a tight fit to the crinoid calyx implied a long-term interaction. That led them to conclude that the gastropods were relying on the crinoids for food. By the latter part of the nineteenth century, the fact that gastropods typically occupy a position over the crinoids' anal aperture led to the inference of coprophagy (Hinde, 1885; Keyes, 1888a, 1888b).

The interpretation that platyceratids fed on crinoid waste and thus benefited from the association persisted through the twentieth century (e.g., Clarke, 1908; Bowsher, 1955; Lane, 1978; Meyer and Ausich, 1983; Boucot, 1990). Under that scenario, it has been generally assumed that the impact on the crinoid was neutral and, thus, that the interaction represented commensalism (Keyes, 1888a; Bowsher, 1955; Lane, 1978; Meyer and Ausich, 1983). Wood (1980, p. 110) considered that the crinoid might have benefited from a coprophagous gastropod by being provided with a "competent elimination system…"—clearly arguing that this represented a case of mutualism. Thomas (1924, p.451), on the other hand, argued that crinoids "were unquestionably the unhappy hosts of a weighty and persistent parasite." Likewise, Clarke (1921, p. 64) suggested that the interaction represented parasitism: "… [The] gastropod…must have been obnoxious to it [the crinoid] as it interfered with the normal alimentary function." More recently the parasitic interpretation has gained support from a number of studies

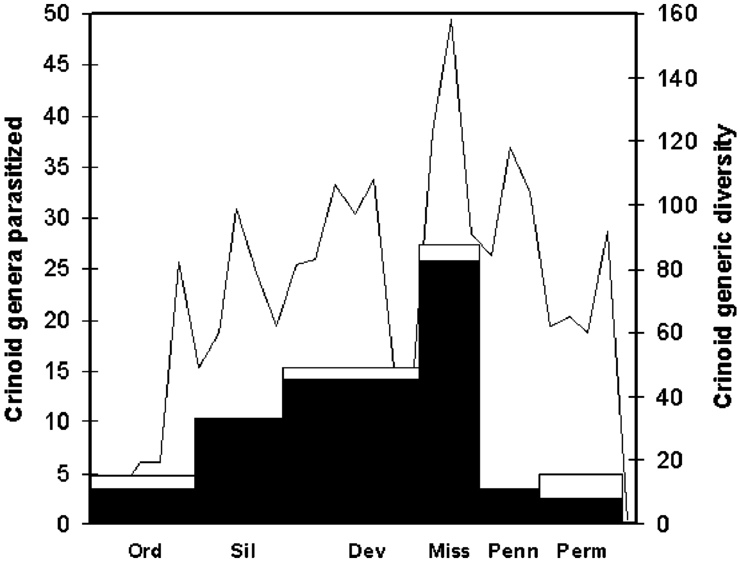

FIGURE 3—Distribution of crinoid genera parasitized by platyceratids during the Paleozoic. Solid bars represent co-occurrences of crinoids and platyceratids; open bars represent inferred associations based on trace fossils (platyceratid growth scars). The upper curve represents Paleozoic crinoid generic diversity based on data from Sepkoski's unpublished compendium.

including those of Lane (1984), Rollins and Brezinski (1988), Baumiller (1990, 2001), Gahn and Baumiller (2001), and Gahn et al. (in prep.).

Although coprophagy has been the most commonly invoked behavior for the infesting gastropods, other ideas about how they may have benefited from crinoids have also been proposed. For example, Lane (1984) suggested that gastropods fed on crinoid gametes that were shed through the anal vent. This idea is supported by the fact that whereas the gametes of modern crinoids are found on their proximal arms in specialized genital pinnules, such pinnules have not been found among Paleozoic crinoids. Lane argued that those crinoids must have shed their gametes through the anal vent, which was occupied by the gastropod.

Baumiller (1990, 2001) also argued that gastropods positioned over the crinoid anal opening could have fed on more than just crinoid excreta; for example, they may have stolen undigested nutrients from their host, and thus have been kleptoparasitic. He supported this claim of kleptoparasitism by noting that among extant comatulid crinoids, the captured and still largely undigested food travels rapidly to the hindgut (Holland et al., 1991), where most digestion occurs. If this were true of Paleozoic crinoids, infesting gastropods could reach through the anal opening into the hindgut with their proboscis and extract undigested nutrients. The kleptoparasitic scenario was recently quantified using a cost-benefit analysis (Baumiller 2001).

Effect of interaction on platyceratids.—Coprophagy, gametophagy, and/or kleptoparasitism represent plausible modes of obtaining nutrients by the infesting platyceratids. Moreover, each predicts that a platyceratid occupying the anal vent, and thus having access to nutrients, was at an energetic advantage relative to a conspecific that had no such access. A recent description of multi-gastropod-infested crinoids (Baumiller, 2002) provides a test of this prediction and thus a rare opportunity to demonstrate explicitly the advantages to infesting individuals.

The crinoid-platyceratid association is generally characterized by a single gastropod positioned on the crinoid tegmen; only a few instances of multi-infested crinoids have been reported. Baumiller (2002) described two specimens of the crinoid *Arthroacantha* with multiple gastropods attached. On one of these, the largest gastropod was positioned directly over the anal vent with 6 smaller gastropods attached in close proximity to the vent. The larger size was interpreted as a reflection of greater rate of growth—a direct consequence of access to crinoid waste, gut, gametes, or any combination of these—and demonstrates the advantage to the infester.

Effect of the interaction on crinoids.—Although in the *Arthroacantha*-platyceratid example cited above, the infesting organism was shown to have gained an “advantage” by virtue of its position over the crinoid anal vent, determining whether the interaction involved mutualism, commensalism, or parasitism requires knowledge of the effects on the host. One feature of the host that may be affected by the presence of an infester, and that is readily quantifiable, is size: if infested crinoids are smaller than uninfested ones, then parasitism is supported. Rollins and Brezinski (1988) used this logic to assess whether infesting gastropods had a detrimental effect on crinoids. Using four crinoid ‘stands’, they measured the size of infested and uninfested calyces of the crinoid *Platycrinites*, and found that infested individuals were on average smaller than uninfested ones, suggesting that parasitized crinoids were negatively affected. This elegant approach was hindered by the small sample size (infested N = 11 and 1, uninfested N = 6 and 3) and the fact that the comparison involved infested individuals from one set of crinoid ‘stands’ and uninfested individuals from another set of ‘stands’. Due to the small sample, the average size differences were not statistically significant. Although statistically inconclusive, the Rollins and Brezinski (1988) study was suggestive of parasitism and provided a methodological blueprint for future studies.

A large collection of two species of Devonian camerate crinoids allowed for a statistical test of the size effect of infestation on the hosts (Gahn et al., in prep.). By comparing infested and uninfested specimens of two species of crinoids, *Corocrinus* and *Gennaeocrinus*, the authors will show that infested individuals were significantly smaller than uninfested ones (Fig. 4). The differences are interpreted as indicating slower growth rates or higher mortality rates of infested crinoids. This detrimental effect of platyceratids on their hosts supports the parasitic, nutrient-stealing hypothesis.

Evolutionary consequences of platyceratid parasitism on crinoids.—The above observations indicate that platyceratid gastropods represented a biological "hazard" to crinoids. In the context of the hypothesis of escalation (Vermeij 1977, 1980, 1987), organisms that have enemies, be they predatory or parasitic, are expected to respond evolutionarily to these hazards. Given that the association between crinoids and platyceratids was geologically long-lived, one might predict a crinoid response. A study by Gahn and Baumiller (2001) provides a test of this prediction.

Gahn and Baumiller (2001) suggested that one potentially effective anti-infestation feature of crinoids was a long, slender anal tube. These authors argued that shifting the gastropod's point of access to the apex of the tube would, among other things, have made it difficult for gastropods to position themselves over the anus.

To test the effectiveness of the tube as anti-infestation device, Gahn and Baumiller (2001) categorized crinoids as 1) tube-bearing, infested; 2) tubeless, infested; 3) tube-bearing, uninfested; or 4) tubeless, uninfested—and showed that the distribution of platyceratids was not independent of the presence of the tube (chi square P = 0.007). Platyceratids were associated almost exclusively with tubeless crinoids.

Gahn and Baumiller (2001) also explored the evolutionary scenario that the tube evolved in

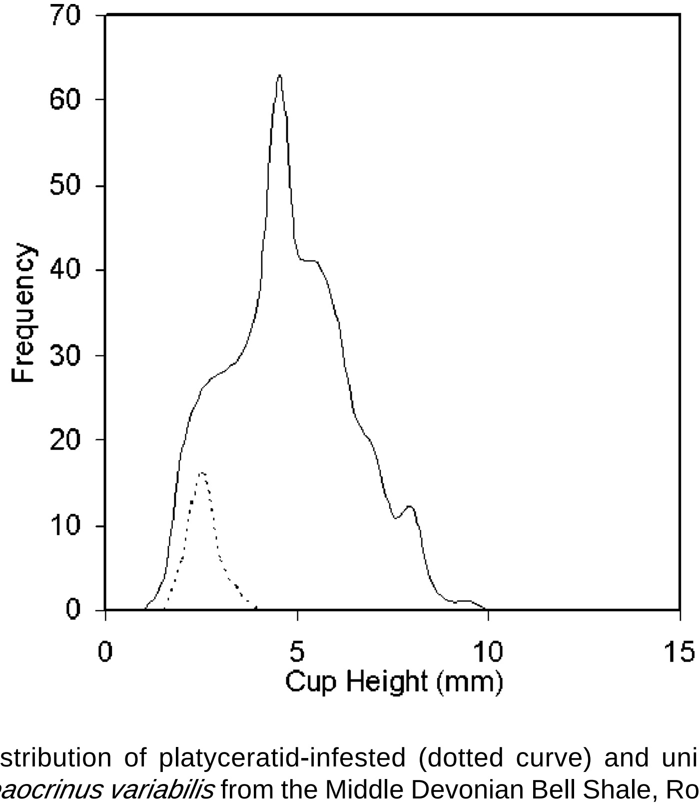

FIGURE 4—Size distribution of platyceratid-infested (dotted curve) and uninfested (solid curve) specimens of *Genneaocrinus variabilis* from the Middle Devonian Bell Shale, Rockport, Michigan. The difference is statistically significant; infested individuals (N = 30) averaged 2.4 mm in height whereas uninfested specimens (N = 396) averaged 4.5 mm (t-test, P<0.001).

response to parasitism. A phylogenetic analysis using 26 genera of monobathrid camerates showed that: 1) the most parsimonious distribution required 4 independent events of tube evolution, and 2) that the tubeless sister taxa of tubed crinoids were infested by platyceratids, while the tubed crinoids were generally uninfested.

The results of the Gahn and Baumiller (2001) study were consistent with the hypothesis that the tube evolved in response to parasitism; but escalation goes a step further and invokes an arms race. Thus, adaptations that counter the effectiveness of enemies should be rendered ineffective by morphological or behavioral evolution of those enemies. Did platyceratids counter the evolution of exaggerated anal tubes with such changes? Baumiller (1990) reported numerous individuals of the Mississippian batocrinid crinoids, *Batocrinus icosidactylus* and *Batocrinus irregularis*, with circular, cylindrical to tapered holes penetrating the plates of the tegmen at the base of a long, slender, multi-plated tube with an anal opening at its apex (Fig. 5). A sectioned specimen of another tube-bearing Mississippian batocrinid, *Macrocrinus mundulus*, infested by a platyceratid, revealed a hole in the base of the tube directly beneath the gastropod. The presence of U-shaped attachment scars, rare instances of multiple holes, and healed (or incomplete) holes was used as evidence that the holes in crinoids did not represent predation, but parasitism. Furthermore, it indicates that the tube was not a foolproof strategy of escape from infestation by snails, as it could be countered by drilling. If platyceratid drilling evolved in response to the evolution of the tube, the “tit-for-tat” would represent a case of escalation.

PLATYCERATIDS AS PARASITES ON OTHER TAXA

Crinoids are not the only echinoderm group associated with platyceratids. Several instances of platyceratids attached to blastoid calyxes are known, including two Devonian and two Mississippian examples (Fig. 6). Levin and Fay (1964) described several specimens of *Diploblastus kirkwoodensis* (Mississippian), each with a small

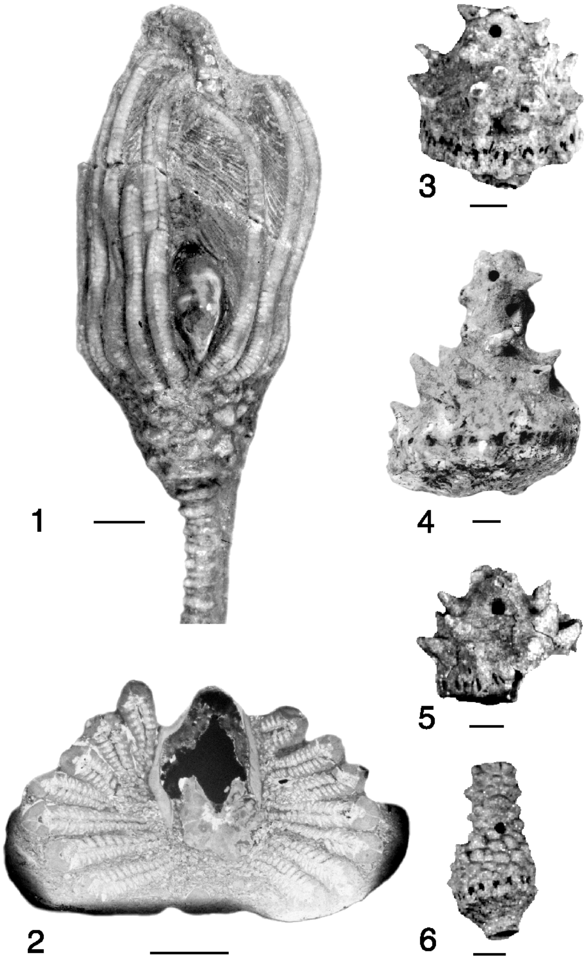

FIGURE 5—Examples of Mississippian batocrinid crinoids with drillholes. Scale bar = 0.5 cm. 1, *Macrocrinus mundulus* (P19426), lateral view of specimen. Note the long anal tube extending beyond the tips of the arms and the platyceratid positioned on the tegmen between the arm bases. 2, Photomicrograph of ground section of same specimen. 3, *Batocrinus icosidactylus* (P19402), lateral view showing drillhole at base of broken-off anal tube. 4, *Batocrinus icosidactylus,* lateral view showing two complete drillholes near base of anal tube. 5, *Batocrinus icosidactylus* (P19394), lateral view of partial calyx with complete drillhole. 6, *Batocrinus irregularis* (P19393), lateral view of specimen with a robust tube penetrated by drillhole. All specimens housed in the Field Museum of Natural History, Chicago, Illinois.

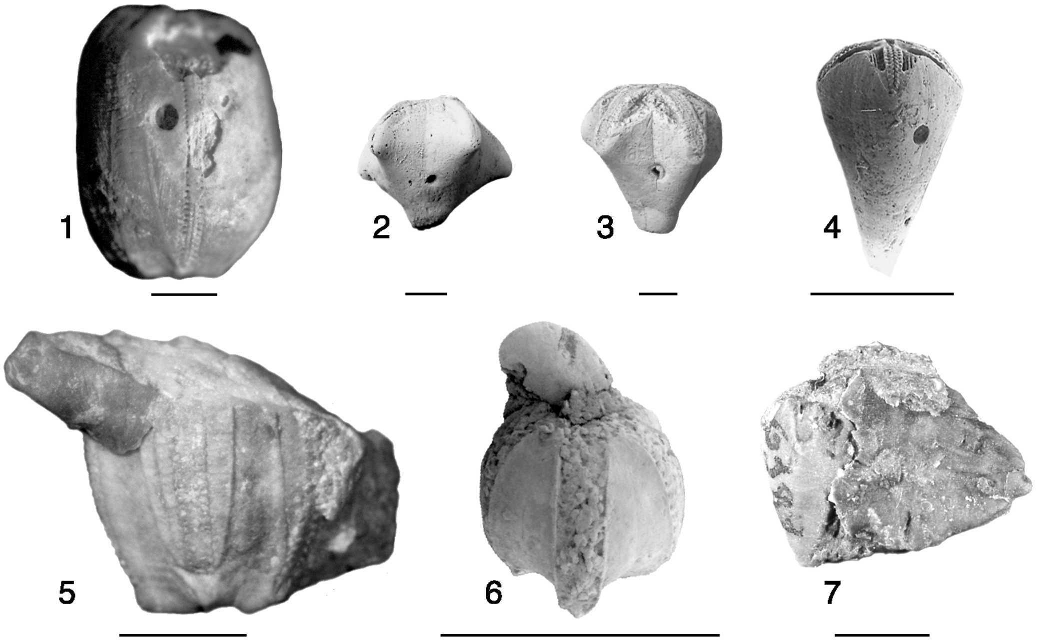

FIGURE 6—Examples of blastoid-platyceratid association (5,6,7) and blastoids with drillholes (1,2,3,4). Scale bar = 0.5 cm. 1, *Nucleocrinus verneuilli* (OSU 14516) with complete drillhole, Columbus Limestone, Middle Devonian. 2, *Orophocrinus stelliformis* (MCZ 360) with complete drillhole, Burlington Limestone, Mississippian. 3, *Orophocrinus stelliformis* (MCZ 144) with incomplete or healed drillhole, Burlington Limestone, Mississippian. 4, *Heteroschisma canadense* (A. Fabian personal collection), Hungry Hollow Formation, Middle Devonian. 5, *Nucleocrinus* sp. with attached platyceratid (J. Topor personal collection), Rockport Quarry Limestone, Middle Devonian. 6, *Diplocrinus kirwoodensis* with an attached platyceratid (WUPM), Saint Louis Limestone, Chesterian. 7, *Heteroschisma subtruncatus* (USNM 481253) with an attached platyceratid, Thunder Bay Formation, Middle Devonian. Repositories: OSU–Ohio State University Natural History Museum; MCZ–Museum of Comparative Zoology, Harvard University; WUMP–Washington University Paleontology Museum.

Platyceras attached to the blastoid calyx. Several specimens of Mississippian *Pentremites* with attached platyceratids have also been reported (Meek and Worthen, 1868; Thein and Nitecki, 1974; Kelly, 1984), and an additional dozen specimens are housed in the collections of the UMMP. Much more rare are cases of Devonian blastoids with platyceratids: such specimens include *Nucleocrinus* and *Heteroschisma* (Baumiller, 1996). These latter specimens are especially important to the interpretation of the interaction between platyceratids and blastoids. Whereas Levin and Fay (1964), noting the position of the gastropods over the anal vent of specimens of *Diploblastus*, concluded that they were coprophagous, which would indicate that the interaction was either mutualistic or commensal, a parasitic interpretation has recently been offered (Baumiller, 1993, 1996; Baumiller and Macurda, 1995). These authors illustrated numerous cases of drilled blastoids. Most commonly drilled were specimens of nucleocrinids, *Heteroschisma*, and the Mississippian blastoid *Orophocrinus*. As is the case with holes in crinoids, the blastoid holes are typically single, circular in plan view with a diameter greater than 1 mm (range 0.3–2.5 mm), complete, and straight-sided to tapered. The known association of platyceratids with blastoids, especially with the two drilled taxa, *Nucleocrinus* and *Heteroschisma*, and the documented drilling of crinoids by platyceratids led the authors to argue that the blastoid holes were produced by these gastropods (Fig. 7). They suggested that the rare presence of doubly-drilled blastoids and the occasional incomplete/healed holes argued against predation, and instead for a long-term association. In addition, the position of the holes away from the anal vent was used to argue against coprophagy; instead, a hypothesis of nutrient-stealing was proposed. This parasitic hypothesis is yet to be tested explicitly, but if it stands up to scrutiny, the blastoid-platyceratid interaction may be worth examining in the context of escalation.

One other example of a platyceratid-echinoderm association is found in the Silurian and involves the platyceratid *Naticonema* and the cystoid *Caryocrinites* (Clarke, 1908; Bowsher, 1955; Kluessendorf, 1983). As in other instances of infested pelmatozoans, the gastropod is found attached to the theca of the cystoid; this has been interpreted as reflecting the coprophagous habit of the gastropod and thus a commensal or mutualistic relationship. However, based on the evidence from crinoids and blastoids, a parasitic interpretation is equally plausible.

CONCLUSION

The list of examples of parasitism in the fossil record is extensive. Distinguishing parasitism from predation, commensalism, or mutualism requires (1) evidence of a long-term relationship between two organisms, (2) demonstration of how the interaction benefits the parasite, and (3) demonstration of how it is detrimental to the host. Only in exceptional cases can these requirements be fulfilled. One example that provides much information on parasitic interactions involves platyceratids and crinoids. This association has recently been re-interpreted as parasitic rather than commensal. The fact that platyceratids were geologically long-lived (Ordovician to Permian), abundant, occurred in a broad range of marine settings, and are known to be associated with a variety of taxa (crinoids, blastoids, cystoids, brachiopods), implies that the parasitic habit may have been common during the Paleozoic. Furthermore, because platyceratids have been

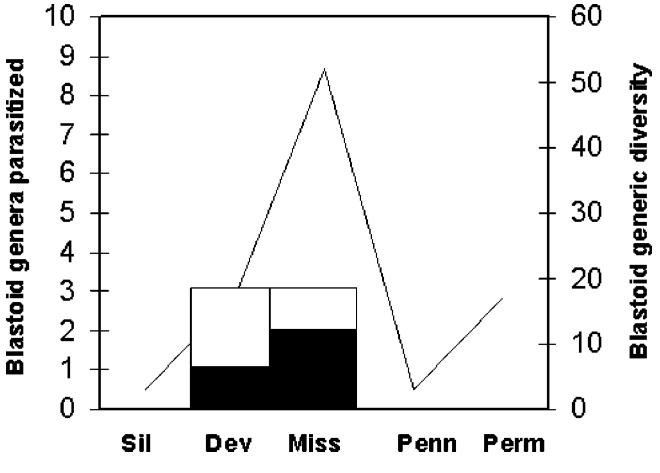

FIGURE 7—Distribution of blastoid genera parasitized by platyceratids during the Paleozoic. Solid bars represent co-occurrences of crinoids and platyceratids; open bars represent inferred associations based on trace fossils (platyceratid growth scars). The upper curve represents Paleozoic blastoid generic diversity based on data from Sepkoski's unpublished compendium.

shown to be capable of drilling their hosts, it may be more appropriate to begin with parasitism, rather than predation, as the "null-hypothesis" for the many boreholes in Paleozoic invertebrates. The consequences of parasitism, like predation, may lead to escalation, and the association of platyceratids and crinoids, and possible other hosts, may provide a rich data source for testing this evolutionary hypothesis.

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