Predation, resistance, and escalation in sessile crinoids

by

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Dedication

To Mark.

“We shall swim out to that brooding reef in the sea and dive down through black abysses to Cyclopean and many-columned Y’ha-nthlei, and in that lair of the Deep Ones we shall dwell amidst wonder and glory for ever.”

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Abstract

Predation, resistance, and escalation in sessile crinoids

V. J. Syverson

Chair: Tomasz K. Baumiller

As animal life diversified over the course of the Phanerozoic, the intensity of predator-prey interactions increased in several phases. Crinoids (Phylum Echinodermata: Class Crinoidea) were a dominant constituent of Paleozoic shallow marine faunas and constitute a lesser component of post-Paleozoic faunas; as most of them are sessile suspension feeders, they provide a good case study for the effect of increasing predation pressure on the Paleozoic evolutionary fauna. Herein are presented injury frequencies and examples of anti-predatory adaptations from a variety of modern and fossil crinoids. New measurements of relative frequencies of injury and regeneration in particular populations of Paleozoic and Recent crinoids are discussed with reference to those from previous studies.

Rates of regenerating injuries in the modern sessile bathyal crinoid *Holopus mikihe* are shown to be comparable to those of shallow-water Mesozoic relatives and many Paleozoic taxa, and lower than all other injury rates measured in living crinoids. Growth and turnover in this species are demonstrated to be very slow; the average adult is 40-50 years old, as compared to 10-20 years in other extant deep-water crinoids. Regenerating injuries on disarticulated spines of Paleozoic crinoids similarly show an increase in regeneration frequency between the Paleozoic and Recent, as well as changes within the Paleozoic.

We present evidence for transitions in the effects of predatory pressure on crinoids at the Silurian-Devonian, Devonian-Mississippian, Middle-Late Mississippian, and Pennsylvanian-Permian based on the occurrence of anti-predatory adaptations. Changes in arm branching morphology that increase resilience to predation are shown to have begun in the Early Paleozoic and reached their maximum by the Early Devonian; on this basis we infer that predators had an influence on crinoid evolution beginning in the Ordovician or Silurian, long before the appearance of the predatory vertebrates and echinoids known to prey on crinoids during later times. Beginning in the Devonian, snails parasitizing crinoids are associated with more frequent crinoid arm regeneration and with the presence of spines on the oral surface near their usual position, consistent with the hypothesis that the snails were targeted by predators with crinoids incurring collateral damage. Calyx spines were common in the Devonian and less common in the Mississippian, suggesting they were associated with predation by placoderms, but tegmen spines associated with predation on parasitic snails persist up to the Late Mississippian. Based on the number of spiny genera and frequencies of spine regeneration, we infer that predation on crinoids decreased into the Permian. Our results support the hypothesis that escalation in the crinoid-predator relationship occurred during the Paleozoic during several different episodes of escalation related to new ecological developments. However, rather than a consistent upward trend in all types of defensive adaptations, we find that some defenses may be associated with types of hostile interaction that later lost ecological importance.

Chapter I.
Introduction

Predatory interactions in the fossil record

Documenting the patterns of change in biotic interactions in fossil ecosystems would seem at first inspection to be an intractable problem. Bias against the preservation of soft-bodied organisms, the variety and flexibility of biotic interactions that lead to surprises even from well-known living organisms, and the difficulty of preserving behavioral traits all contribute to this problem. Despite these difficulties, the traces of some biotic interactions, such as predation, parasitism, mutualism, and epibiosis, are found in the metazoan fossil record with enough frequency to attest to their continued presence, and to allow inferences to be drawn in some cases about their influence on the history of life.

After epibiosis, predator-prey interactions are the next-easiest to document. Most of the primary evidence for predator-prey interactions in marine environments, the main subject addressed in this volume, comes from either characteristic lethal damage or from partially-healed nonlethal injuries preserved in the hard parts of prey organisms. In either case, the identity of the predator usually remains conjectural. Secondary evidence must therefore support the bulk of any argument, usually in the form of frequencies of taxa bearing adaptations whose purpose can be convincingly reconstructed as predatory or anti-predatory. Although biotic interactions are undoubtedly an important force in structuring modern ecological communities, and are coarsely correlated in the fossil record with marine taxonomic diversity (Huntley and Kowalewski 2007), their role in determining the course of life's history on a macroevolutionary scale is still somewhat unclear.

Escalation and marine revolutions

A particular formulation of the idea that antagonistic biotic interactions have been the major influence on the history of life is referred to as "escalation", following Vermeij (1987). According to the escalation hypothesis, the intensity of predator-prey interactions has increased over the Phanerozoic, predicting a general trend toward more powerful offensive and defensive adaptations among dominant taxa through time, as well as the banishment of slower or weaker taxa to marginal environments. It is generally agreed that predation has intensified over the course of the Phanerozoic (Bambach 1993). But did this increase occur simultaneously across different interactions, or did some arms races occur earlier and others later? Did escalation occur constantly, or in episodes? What was the effect of mass extinctions?

Escalation may have occurred in episodic bursts, rather than continually. The first of these episodes to be identified was the "Mesozoic Marine Revolution" (Vermeij 1977), in which a variety of new feeding strategies (*e.g.*, Aristotle's lantern, shell-peeling claws, reef-browsing beaks) and anti-feeding strategies (*e.g.*, infaunalization, swimming, shell remodeling) simultaneously became more common over the middle to late Cretaceous. Subsequently, a "Middle Paleozoic Marine Revolution" was identified on the basis of an apparent coordinated increase in the diversity of durophagous predators and the proportion of taxa with anti-predatory adaptations in the Middle Paleozoic, specifically the Devonian through Carboniferous (Signor and Brett 1984). Active nektonic predators, particularly placoderms and nautiloids, radiated at the expense of planktonic and demersal diversity (Bambach 1999; Klug et al. 2010); some indications of a secular increase in ocean oxygenation 390 million years ago suggest that this radiation may have been related to the increased availability of oxygen for metabolism (Berner 2006; Dahl 2010). Among durophagous predators, the gnathostomes, phyllocarids, and eumalacostracans underwent radiations. Predatory ammonites, coleoids, and cidaroid urchins also appeared during this interval. Coincident with these radiations, an assortment of predation-resistant morphologies became more frequent in other marine taxa, due to a combination of extinction and radiation: disjunct coiling vanished among molluscs while sculpture increased, crinoids acquired spines and thicker calycal walls, and spiny productid brachiopods diversified.

Crinoids and antagonistic biotic interactions

General anatomy and natural history of the taxon

Crinoids, the most ancient and basal extant class of echinoderms, are sessile or slow-moving suspension-feeders with robust endoskeletons composed of many small elements (ossicles) of porous calcite (stereom). A brief overview of generalized crinoid anatomy will be given here as an orientation for the coming discussions of anti-predatory morphological adaptations; for a diagram, see Figure I-1 (Ubaghs et al. 1978). Due to radial symmetry, echinoderm morphology is usually discussed using the directions *oral* (or *adoral*) and *aboral*, denoting respectively the side containing the mouth and the side away from the mouth. The body is usually divided into the crown and the stalk; some extinct and many modern species are stalkless. The crown is composed of a cup, or calyx, in which most of the internal organs are housed, and some number of radially-positioned and bifurcating arms, which are extended into the current during feeding. Ecologically, all known crinoids are epifaunal suspension-feeders; their food consists of suspended particles pulled from the water column by a double row of tube-feet arrayed along the oral side of the arms, which filter food particles from the water column and pass them inward to the mouth. In some crinoids, the articulations between the arm ossicles contain muscles, while in others, their position is passively controlled by mutable collagenous tissue. The mouth is located centrally on the cup between the arms on the oral surface, which is called the tegmen; the aboral side is usually positioned facing into the current. The cup is composed of ossicles that articulate or fuse to form a cavity containing the central organs of the digestive, circulatory, and nervous systems. The anus is positioned off-center on the oral side; in many extinct taxa, its opening is elevated above the tegmen on a tube or surmounted by a structure called an anal sac, which may have contained the gonads or an extension of the gut. The stalk, where present, extends from the aboral side of the cup, and is variously stiff, flexible, or muscular, depending on the inter-ossicle articulations. The stalk serves to anchor the organism to a substrate, and is sometimes equipped for this function with short finger-like extensions called cirri. Extensive regenerative capacities are universal among the echinoderms: almost any nonfatally lost body parts can be regrown given enough time, and regeneration in both fossil and modern crinoids is well documented.

Basic crinoid taxonomy

The bulk of Paleozoic crinoids are divided by modern authors into four main subclasses, the Disparida, Flexibilia, Camerata, and Cladida (Figure I-2). This excludes a handful of minor taxa, but comprises the large majority of known fossil species. The work presented herein will focus mainly on the numerically and ecologically dominant camerates (Camerata) and cladids (Cladida). Camerates, which are generally characterized by a large, multi-plated, rigid calyx, were the most diverse and numerous subclass in the first half of the Paleozoic. The cladids are paraphyletic, but the so-called "advanced cladids" (Poteriocrinina), which originated in the Middle Devonian and comprise most cladid genera of that age and later, are monophyletic to all other Paleozoic groups (Ausich 1997).

Cladids are presumed to be the ancestors of the sole surviving post-Paleozoic crinoid lineage, the Articulata, which radiated in the Triassic. This subclass is divided into eight orders, of which four (Encrinida, Holocrinida, Millericrinida, Roveacrinida) are extinct, three (Isocrinida, Cyrtocrinida, Hyocrinida) are confined to deep water, and the last (Comatulida) contains the stalkless "feather stars" which comprise more than 80% of all living crinoid species (Hess et al. 2011).

Paleozoic & post-Paleozoic history of the Crinoidea

Crinoids probably arose in the Early Ordovician (Moore et al. 1978) and were major constituents of Paleozoic marine communities starting in the middle Ordovician (Peters and

Ausich 2008). Distinct crinoid faunas are characteristic of times before and after the late-Devonian-through-Mississippian faunal transition: early Paleozoic crinoid assemblages are dominated by the subclass Camerata, while the late Paleozoic is dominated by the subclass Cladida, as seen in Figure I-2 (Webster 2003). During the late Devonian, especially during the Givetian biocrisis, many of the early Paleozoic crinoid species vanished (Ausich et al. 1994; Webster et al. 2005) and were replaced in the early Mississippian (Tournaisian-Viséan) by the simultaneous diversification of the advanced cladids and re-radiation of camerates during the so-called "Age of Crinoids", when some combination of the availability of congenial growing environments and an extinction among predatory vertebrates produced a tremendous increase in both the diversity and the abundance of crinoids (Kammer and Ausich 2006; Ausich et al. 2011; Sallan et al. 2011). In the late Mississippian, the camerates again declined in diversity and abundance; only a few families survived until the end-Paleozoic extinction. The advanced cladids, in contrast, produced the major crinoid groups of the Late Paleozoic (Hess et al. 2011; Janevski 2011).

Although the post-Paleozoic diversification of the Articulata never achieved pre-extinction levels of taxonomic diversity, a comparable level of ecological and morphological diversity was attained fairly rapidly, with substantial convergence onto Paleozoic morphotypes (Ausich 1988; Foote 1999; Hagdorn 2011). Over the course of the Late Cretaceous and Cenozoic, the articulates gradually lost occupancy of the shallow-marine, sessile, epibenthic niche inhabited by most Paleozoic crinoids, and were gradually drawn into their present-day ecological positions: the shallow-marine, mobile niche inhabited by the Comatulida, which are the most diverse and most abundant order of extant crinoids, and the deep-water, sessile to barely-mobile niche inhabited by all living non-comatulid crinoids.

History of predation and parasitism in crinoids

Interactions between crinoids and predators, including fish and echinoids, have occasionally been observed directly in modern ecosystems (Fishelson 1974; Meyer and Ausich 1983;

Schneider 1988; Baumiller et al. 2008), as have crinoid remains in fecal material or gut contents (Meyer 1985; Baumiller et al. 2008). Injuries and regeneration in living specimens are observed much more frequently (Amemiya and Oji 1992; Donovan 1992; Carnevali et al. 1993; Oji 1996, 2001; Lawrence 2009; Baumiller 2013*a*). Although modern crinoids sometimes autotomize arms as part of ontogeny (Roux 1976) or under abiotic stress (Baumiller 2003), partial predation is thought to be the cause of most such injuries in both fossil and modern specimens (Mladenov 1983; Meyer 1985; Oji 1996; Lawrence 2009). Damaged and regenerating body parts may therefore be used to infer the presence and frequency of predation on fossil crinoids as well (Oji 2001; Baumiller and Gahn 2004; Gahn and Baumiller 2005, 2010; Baumiller et al. 2008). The identity of the predators on fossil crinoids is usually unclear, but direct observations implicate fish (Meyer 1985; Gorzelak et al. 2011), sea urchins (Baumiller et al. 2008), and sea stars (Baumiller 2008). While there is no evidence for predation by cephalopods, they are thought to have preyed on trilobites as early as the Ordovician based on gut traces, while radulae are known from the Silurian and chitinous beaks from the Carboniferous (Brett and Walker 2002); as major Paleozoic nektobenthic predators, it is plausible that they may also have preyed on crinoids or crinoid commensals.

Increasing predation intensity in the Middle Paleozoic, combined with the effects of the late Devonian and Mississippian extinctions and recoveries, produced a complex and interlocking set of ecological signals. The interaction between stalked crinoids and their predators is a study system well suited to examining this pattern. Increasing frequencies of interaction between crinoids and predators throughout the Paleozoic are well documented: along with the increases in anti-predatory adaptations noted by Signor and Brett (1984), predatory injuries become more common in camerate crinoids from the Ordovician to the Devonian, and parasitic snails infest them with increasing frequency from the Ordovician to the Mississippian (Baumiller and Gahn 2004). However, no decline was observed in the total number of dense crinoid stands between Ordovician/Silurian and Mississippian assemblages after sedimentological correction (Aronson 1991), suggesting that increasing predation during the intervening period was not an important control on the occurrence of such stands.

Out of the assorted Late Devonian extinction events, the Hangenberg (end-Famennian) extinction was the most important in restructuring vertebrate communities: it removed the dominant Devonian durophagous fishes, the placoderms, which were primarily shearing predators, allowing their replacement by a more modern Mississippian chondrichthyan and actinopterygian fauna, which were generally crushing predators (Long 1995; House 2002; Sallan and Coates 2010). The archaeocidarid urchins, ancestors of the cidaroid urchins known to be modern benthic predators on isocrinids, also originated in the Middle Devonian and had modern durophagous mouthparts by the Carboniferous; they often co-occur with crinoids during the late Paleozoic, sometimes in association with fragmented crinoid ossicles (Schneider 2001; Baumiller et al. 2008). Rates of crushing predation did clearly increase between the Devonian and the Mississippian, as evidenced by angular shell fragments in sediments (Salamon et al. 2014). Evidence for a decrease in predation at the Devonian-Mississippian transition is visible in camerate arm regeneration frequency (Baumiller and Gahn 2004) but is not statistically significant.

The sharp reduction in North American diplobathrid camerate diversity at the end of the Mississippian has been suggested to have been the result of re-radiation of the chondrichthyans into the same durophagous niches previously occupied by placoderms, after which these new predators might have driven their prey to extinction (Waters and Maples 1991; Sallan et al. 2011). Sallan et al. (2011) additionally conclude that the Tournaisian-Viséan peak in crinoid diversity was a reaction among camerates to the disappearance of Devonian predatory fish during the end-Devonian Hangenberg extinction.

The aforementioned Mesozoic Marine Revolution is generally placed in two intervals, the Late Triassic and the Late Cretaceous. The only modern shallow-water crinoids are the highly mobile comatulids, which appeared along with their characteristic swimming behavior in the earlier Late Triassic episode of escalation, possibly in concert with a radiation of benthic predators (Baumiller et al. 2010; Janevski 2011; Gorzelak et al. 2012). During the latter period, stalked crinoids went from being common to being very rare in shallow-water sediments, consistent with observations that predation and regeneration are much more common in deep than in shallow water (Bottjer and Jablonski 1988; Oji 1996; Baumiller 2013*b*), and concurrent with an increase in nektonic predation (Vermeij 1977). Consequently, predation is generally implicated as the most likely cause of these changes as well (Meyer and Macurda 1977).

The apparent unpalatability of modern comatulids to fishes (Fishelson 1974; Meyer 1985; Baumiller 2008) stands in evident contrast to all these observations of predation. Similarly, the low ratio of living tissue to stereom in crinoid arms might suggest that they are a poor food source, especially for metabolically active predators such as fish. In conjunction with the large number of ecto- and endoparasites, commensals, and assorted hangers-on observed in the arms of modern crinoids (Fishelson 1974; Meyer 1985), this has led to the suggestion that some arm-grazing predators may be targeting the commensals and injuring the crinoid as collateral damage (Baumiller 2008). If so, the same might be expected to have occurred in the past.

Although most parasites are small and soft-bodied with low preservation potential (Conway Morris 1981), the Paleozoic snails of order Platyceratida form one important exception. These snails are frequently found on crinoids, usually on the oral surface over the anus, although sometimes over a drilled hole. In some cases the shape of the snail's growing margin conforms to the host's calyx, indicating a long period spent in a single position. Reconstructions of their lifestyle range from filter-feeding to outright predation, but the dominant interpretation places them on the continuum between commensal coprophagy and kleptoparasitism, with possible gametophagy. This system provides a test case for the role of infestors in drawing the attention of predators during the Paleozoic (Brett et al. 2004). Platyceratids are indeed found preferentially on crinoids of the subclass Camerata (Gahn and Baumiller 2003, 2006; Baumiller et al. 2004), which are also more likely to have regenerating arms (Gahn and Baumiller 2010), lending support to the possibility.

Defensive adaptations

An epibenthic, sessile, suspension-feeding lifestyle involves constant exposure to the water column in order to collect food, and therefore leaves crinoids exposed to the attentions of both benthic and nektonic predators. Crinoids have therefore developed a variety of defenses including armor, adaptations to a mobile lifestyle, biochemical defenses, autotomy, and various other morphological optimizations.

Armoring may be achieved with thickened plates, especially in the calyx; with spines, nodules, or other protruding structures located on the vulnerable parts; or, in comatulids with their reduced calyces, by reinforcement of the oral surface with dense, spiny pinnules. Such mechanical defenses might function by strengthening the test, by dispersing bite force on the prey side and concentrating it on the predator side, or by increasing the effective size past some predator's gape width.

Muscles are known to be present in the arms of articulate crinoids and were recently found to have been present in the stalks of the Devonian flexible crinoid *Ammonicrinus* (Gorzelak et al). Stalkless crinoids, such as the comatulids and *Saccocoma*, use muscular arms to crawl or swim in order to hide or escape from both nektonic and benthic predators, while the isocrinids escape by crawling with their arms, dragging the stalk behind (Baumiller et al. 2008). In modern cyrtocrinids, the arm muscles allow the arms to close up in a tight, protective coil, which may also have been the function of the ammonicrinids' flexible stalks. Mobility may also have been achieved by attachment to a mobile substrate (e.g. *Pentacrinites*, *Seirocrinus*) or via various other conjectured means (e.g. *Uintacrinus, Scyphocrinites*) (Seilacher and Hauff 2004).

Comatulids employ biochemical defenses including unpalatability (Rideout et al. 1979; McClintock et al. 1999) and aposematic coloration (Lawrence 2009). Living cyrtocrinids (Kemami Wangun et al. 2010) may have similar adaptations, but none have been detected in isocrinids (McClintock et al. 1999). These adaptations are usually associated with a particular group of organic compounds called phenanthroperylene quinones, which therefore have been used as indicators for such chemical defenses in fossil taxa. The diagenetic products of these polyaromatic quinone compounds have been isolated from Mesozoic fossil millericrinids and encrinids (Wolkenstein et al. 2006), indicating that the capacity to manufacture these molecules is widespread among at least the Articulata. Quinones have also been recovered from several more taxonomically-distant Mississippian specimens (O'Malley et al. 2013), indicating that manufacture of the potentially pigment- or taste-related quinones is a generally-held capacity among both modern and fossil crinoids, and the crystal structure of echinoderm ossicles suggests that they may be recoverable from many other fossil crinoids.

Autotomy, the ability to deliberately shed the arms or stalk, has been observed in the Articulata as a strategy for escaping from predators (Oji and Okamoto 1994; Baumiller et al. 2008). In articulates, autotomy occurs at specialized inflexible articulations between ossicles, which are usually dispersed at regular intervals through the stalk (Donovan 1990). Some Paleozoic crinoids may also have been able to autotomize their arms (Baumiller 2008) or stalks (Baumiller and Ausich 1992; Donovan 2012).

Assorted other morphological traits also improve resilience to predation. For instance, the gonads are located in the arms in modern comatulids, far from any area that might be fatal when attacked, and may have been elevated into an anal sac in cladids for similar reasons (Lane 1984). Reduction of the size and complexity of the calyx may also have some defensive significance, as conjectured by Sallan et al. (2011), but the precise function of these traits is unclear (Simpson 2010).

Summaries of the following chapters

The preceding background covers how interactions with predators have structured the evolution of crinoids throughout the entire history of the clade. The aims of the work described in this dissertation were to compare the population dynamics and injury rates of fossil and extant sessile crinoids, and to clarify the progression of evolutionary events between crinoids and their predators and parasites associated with episodes of marine escalation.

Chapter II describes observations of a population of the cyrtocrinid *Holopus mikihe* in a modern community from a deep-water Caribbean reef near Honduras. The Cyrtocrinida, an order of articulate crinoids characterized by sessile, cemented habit and robust, simplified skeletons, were highly diverse and common in shallow water during the Mesozoic, but have been reduced to a handful of deep-water genera in the present day. Because predation is implicated in the Cenozoic retreat of sessile and stalked crinoids into the bathyal habitat (Meyer and Macurda 1977; Salamon and Gorzelak 2007; Wisshak et al. 2009), comparisons between the frequency of injury in *Holopus* and that in other modern and fossil populations are useful. The presence of distinct subadult and adult ontogenetic stages is also noted here for the first time, and the average adult age is estimated at ~50 years, substantially older than in other living crinoids for which age estimates exist.

The remaining chapters focus on Paleozoic crinoids. In Chapter III, we introduce *estimated arm loss* (EAL), a measure for the vulnerability of crinoid arms to predation following Oji and Okamoto (1994). Frequency of injury in camerates is inversely correlated with EAL, which, if we assume no differences in growth rate, implies that it took them a shorter time to regrow completely (Baumiller 2013), indicating its possible association with predation intensity. EAL shows a sharp downward trend in the early Paleozoic, consistent with reaction to increasing predation, as predicted by the escalation hypothesis. However, this effect is only apparent in the Camerata, the dominant subclass of the early to middle Paleozoic; the measure is constant in the other Paleozoic subclasses. The trend also reaches its end by the Early Devonian, which is the beginning of the Middle Paleozoic Marine Revolution as originally construed.

Evidence of predation in Paleozoic crinoids is the subject of Chapter IV. Measurements of regenerating spines from Pennsylvanian cladids are used to calculate their frequency of injury before peri- and post-mortem breakage. These values are compared to frequencies of injury and regeneration observed in other living and fossil crinoid populations.

In Chapter V, the record of temporal ranges of spiny crinoid genera, as used in the original description of the Middle Paleozoic Marine Revolution, is re-compiled with the addition of anatomical detail on the location of the spines. This allows the timing of peaks in spinosity to be correlated with other events associated with the MPMR.

Figures

Figure I-1. Diagram of generalized crinoid anatomy. (A) Large-scale anatomy of a typical Paleozoic stalked crinoid. (B) Cup anatomy of a similar generalized Paleozoic crinoid. Illustrations by VJS.

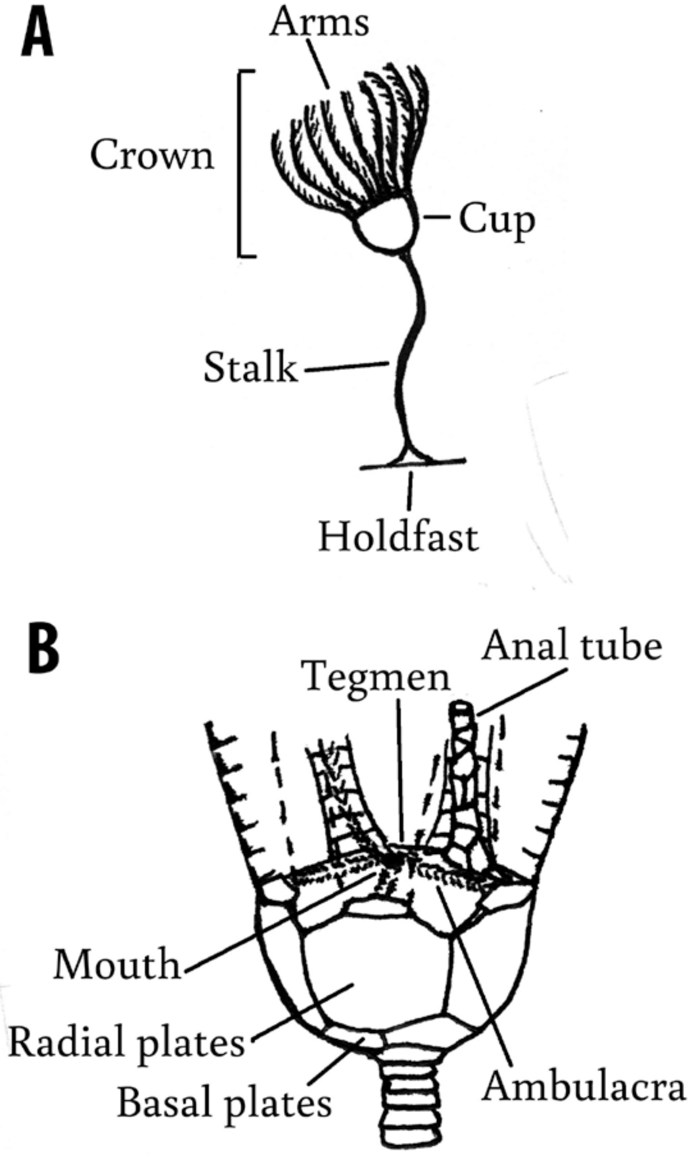
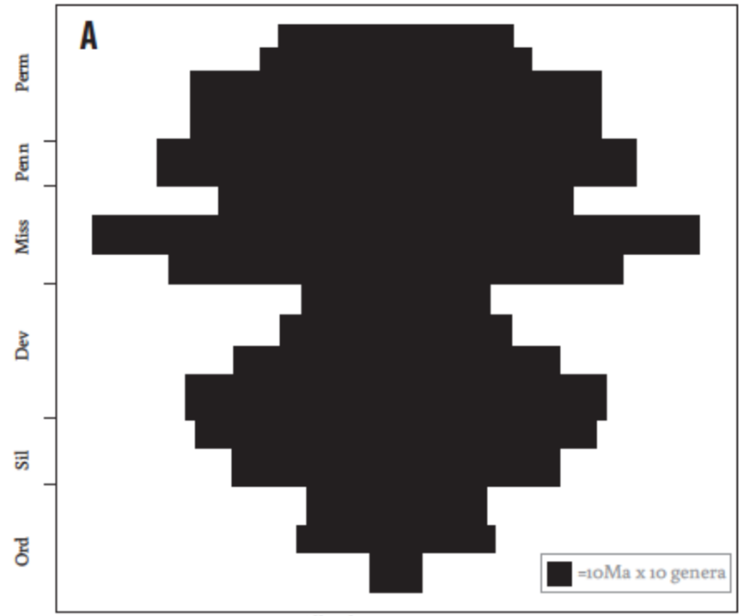
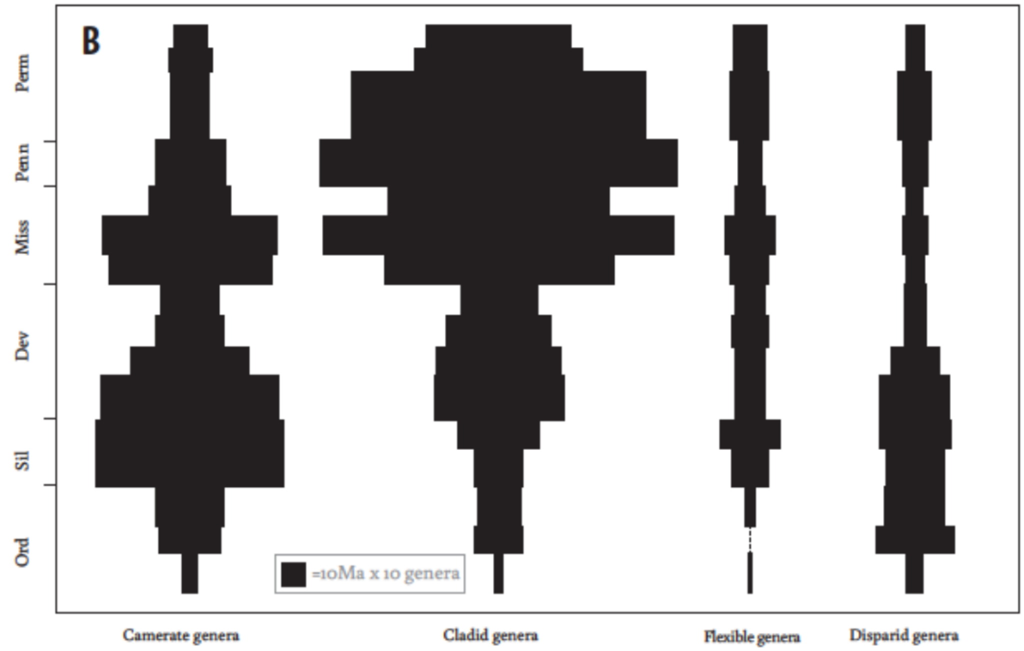


Figure I-2. Generic diversity of Paleozoic crinoids. A. Generic diversity of all crinoids during Paleozoic. B. Generic diversity of Camerata (left) and Cladida (right) during Paleozoic. All taxonomy and ranges follow Webster (2003).



All Paleozoic genera



Chapter II.

Growth, injury, and population dynamics in the extant cyrtocrinid *Holopus mikihe* (Crinoidea, Echinodermata) near Roatán, Honduras

V. J. Syverson, Charles G. Messing, Karl Stanley, Tomasz K. Baumiller

Abstract

The crinoid order Cyrtocrinida is mainly known from Mesozoic fossils; its few surviving members, all from bathyal environments, constitute perhaps the most peculiar living group of crinoids. Cyrtocrinids attributed to *Holopus mikihe* (Donovan and Pawson 2008) have been observed in large numbers via submersible off the western coast of Roatán, Honduras, on vertical and overhanging walls at depths between 430 and 640 m. Observations in 2012, 2013, and 2014 have permitted the first estimates of population structure, growth, and regeneration. Two size modes were observed; the flat barnacle-like juvenile stage resembles confamilial and co-occurring *Cyathidium pourtalesi*, whereas the larger “adults” elevate the crown on a stump-like calyx. Overall maximum (99th percentile) growth rate was 0.19 cm y^{-1}, giving a minimum predicted age of 16 y for the largest specimen and 8.7 y for the median specimen; the median growth rate was 0.04 cm y^{-1}, corresponding to 72 y and 39 y. However, the slower rate of growth in juvenile as compared to adult specimens means that these ages are underestimates; true median age may be closer to 50 y. Arm regeneration rate is estimated at 0.6 cm y^{-1}, and 9.8% of adult individuals were visibly injured, giving an average interval of about 1.4 y between arm loss events. No recruitment or mortality was observed, and aggregations of evenly-sized individuals were prevalent, consistent with sporadic local recruitment and mortality.

Introduction

Cyrtocrinids are a highly derived order of sessile articulate crinoids characterized by cementation to a hard substrate, with the column either short or entirely absent (Hess, Messing, and Ausich 2011). Although the origins of the group are obscure, they are thought to be monophyletic based on both morphological and molecular evidence, and to have diverged from their closest relatives, the hyocrinids, at about 187 Ma (Rouse et al. 2013). Cyrtocrinids originated in the Triassic (Salamon, Gorzelak, and Zatoń 2009), radiated during the Middle Jurassic, and remained highly diverse and successful into the Early Cretaceous, with 15 families and numerous species (Hess, Messing, and Ausich 2011), and habitats ranging from shallow (Baumiller and Gaździcki 1996; Donovan and Jakobsen 2004) to deep (Charbonnier et al. 2007; Wisshak et al. 2009) water. Figure II-1 shows the generic diversity of the order (A) and its three constituent superfamilies (B). They covered the gradient of habitat depth either until the end of the Mesozoic or well into the Paleogene, depending on paleoenvironment reconstruction (Donovan and Jakobsen 2004; Wisshak et al. 2009). If the former, they may have been driven out of shallow environments by further increases in predatory pressure from the Paleogene teleost radiation (Bottjer and Jablonski 1988; Vermeij 1993), possibly in combination with the end-Cretaceous extinction; if the latter, some may have remained in protected shallow-water relict communities. In either case, as a result of the poor fossilization potential of deep-water habitats, the fossil record of the cyrtocrinids is entirely unknown between the Miocene and the Recent.

Only three cyrtocrinid families are known to have survived past the Mesozoic. Four extant genera have been found, all living in deep water. Of these, *Neogymnocrinus* and *Proeudesicrinus* are known only from New Caledonia (Améziane-Cominardi et al. 1990); each is the sole post-Mesozoic representative of its family (Sclerocrinidae and Eudesicrinidae, respectively) (Hess, Messing, and Ausich 2011). The two genera constituting Holopodidae are more widely distributed across the fossil record as well as the modern ocean: living *Holopus* has been found in the Caribbean as well as in New Caledonia, and *Cyathidium* in the

Caribbean, the Azores, and the Comoros (Améziane-Cominardi 1999), and both are known from Jurassic through Miocene strata of Europe.

Holopodidae are characterized by the lack of a column, cementation of the calyx directly onto a hard substrate, and the ability to coil the arms tightly. The skeletal and soft-tissue anatomy and histology of modern *Holopus* and *Cyathidium* have been described in great detail from collected specimens (Carpenter 1884; Grimmer and Holland 1990; Donovan 1992; Heinzeller and Fechter 1995; Améziane-Cominardi 1999). Donovan and Pawson (2008) comment on the substrate affinities and direction of growth with respect to current in *H. mikihe* and *H. rangii*. However, due to their cryptic habitat, there has been little other research on the ecology of these organisms, and most aspects of life history in extant cyrtocrinids remain largely unknown.

Growth rates and regeneration frequencies in other crinoid taxa

Directly measured growth rates of several non-comatulid crinoid species have been used to estimate individuals' ages. Table 1 lists collection depths and estimated ages of measured specimens. Some of the methods yielded only a lower bound on the age of the oldest individuals, while others made it possible to estimate a mean age for populations.

Observations of autotomy behavior in the isocrinid *Metacrinus rotundus* from Japan indicate that they are fairly robust to mechanical stress: grasping the arm with forceps neither breaks arms nor induces autotomy (Oji and Okamoto 1994). It is therefore generally assumed that regenerating arms in fully developed individuals indicate nonlethal interactions with predators and can be used to estimate predator encounter rates (Baumiller 2013 a). Thus, if rates of regrowth are known, the frequency of nonlethal arm loss can be used to estimate the frequency of interaction with predators. Injury frequencies for a number of fossil and modern crinoid taxa are given in Table 2. In general, fewer injured individuals are seen in fossil assemblages than in living ones. This is due to some combination of taphonomic effects, in which postmortem breakage tends to obscure the visibility of nonlethal injury, and genuinely higher frequencies of predation in present-day marine ecosystems than in similar environments in the geologic past. The magnitude of the former effect is usually on the order of 1% difference (Syverson 2014), whereas the latter is much more significant.

Specimens of the isocrinid *Endoxocrinus* from the tropical western Atlantic show a significantly increased frequency of regenerating arms in shallower water. Individuals collected in depths above 500 m had an average of 25% of their arms injured and regenerating, while those from more than 500 m depth had around 13% of arms injured (Oji 1996). The eastern Pacific ten-armed feather star *Florometra serratissima* also shows higher arm regeneration frequency in shallower water. In the shallowest sample, from 79 m, an average of 18% of the arms of individuals were regenerating, compared to 4% at 208 m and 1% at 1,143 m (Mladenov 1983; Baumiller 2013 b). This is probably at least partially due to the slower growth and regrowth of stereom in cold water (Davies et al. 1972).

The only cyrtocrinids in which injury has been observed are the fossil species *Eugeniacrinites cariophilites* and *Pilocrinus moussoni* from the Late Jurassic. Three of 36 cups (8.3%) had visible bite marks in *P. moussoni*, and “nearly 10%” of 470 cups of *E. cariophilites* were “mutilated”, a term which here includes swelling and atrophy as well as injury; some, however, had visible bite marks (Hess 2014).

Although injury and regeneration are known from collected *Holopus* specimens (one specimen dissected by Donovan (1992) had a regrowing arm, and one pictured in Donovan and Pawson (2008) is visibly injured) no attempt has been made to estimate injury and regeneration frequency in *Holopus*. In this study, we provide the first estimates of growth rates, lifespan, and injury frequency in *Holopus mikihe* based on *in situ* observations of a living population.

Data sources and methods

Location of dives

Data were collected in June 2012, July 2013, and May 2014. Video, still photographs, and several specimens were collected from the submersible *Idabel* at approximately 16°18'N 86°36'W off the coast of Roatán, Honduras, at depths between 430 and 640 m.

H. mikihe was observed on vertical and overhanging surfaces of boulders. Other crinoids collected or observed in the same area are listed in Table II-3. Other hard-substrate organisms included a variety of hexactinellid sponges (e.g., *Farrea*), demosponges (e.g., Desmacellidae, Petrosiidae, Geodiidae, *Spongosorites* sp., *Corallistes* sp.), asteroschematid and other ophiuroids, echinoids (e.g., *Calocidaris mortenseni*, *Plesiodiadema antillarum*), asteroids (e.g., *Novodinia antillensis*), scleractinian corals (e.g., *Dendrophyllia alternata* and numerous solitaries), antipatharians, octocorals (e.g., Primnoidae, Plexauridae, Ellisellidae), sea anemones, stylasterid hydroids, serpulid polychaetes, and various decapod crustaceans (e.g., *Homola* sp., Chyrostylidae). Relatively few bottom-associated fishes were observed, e.g., *Synagrops bellus* (Acropomatidae), *Chaunax pictus* (Chaunacidae), *Ijimaia antillarum* (Ateleopodidae), *Grammicolepis brachiusculus* (Grammicolepididae), *Beryx decadactylus* (Berycidae), *Oxynotus caribbaeus* (Oxynotidae), and Bythitidae.

Methods of data collection

The submersible was equipped with a pair of parallel scaling lasers 10 cm apart. Specimen size was measured at the widest point of the calyx by importing the photograph or video frame into Adobe Illustrator, taking measurements by drawing vector lengths, and comparing calyx diameter measurements (Figure II-2A) to the 10-cm scale bar formed by the lasers (Figure II-2B). The photographs and videos were taken at variable distance from the rock face, such that image scale varies from 0.22 m to 5.12 m in the horizontal dimension. In total, 817 measurements were taken over the three years combined: 273 from 2012, 344 from 2013, and 200 from 2014.

Sixty individuals were observed more than once over the three years of sampling. Growth rates were estimated by year-to-year changes in measurements of these individuals. Our ability to revisit sites was facilitated by two factors: the excellent knowledge of the localities by KS, whose experience includes piloting more than 1200 dives in the submersible at Halfmoon Bay, Roatan since 1998, and the fact that the topography in these sites is highly irregular with many landmarks. Thus while finding particular boulders with Holopus populations proved relatively easy, identifying specific individuals year after year required referring to close-up images from previous years while maneuvering the sub. One individual in which two arms were completely missing in 2012 (Figure II-2C) was photographed in all three years; its visceral mass was apparently uninjured, allowing an estimate of arm regeneration rate alone. No new individuals appeared, and no individuals disappeared, at the revisited sites over the period of observation; no life table, therefore, could be formulated.

In each image measured, the number of visibly injured specimens was noted, along with the number with arms fully opened and the number in good close-up focus. Total image area was calculated for each image as (2/3)((width of scale bar)cos(angle of scale bar from horizontal))^2, which allowed computation of population density per image. All calculations were carried out in R (R Core Team 2014).

Results

Size and spatial distribution

The sizes follow a bimodal size distribution. Kernel density estimation, conducted using the R base function “density” (Gaussian kernel function; smoothing bandwidth = 0.1448), gives the values of these modes at about 0.84 cm and 1.79 cm (Figure II-3A). These size modes correspond to two visually apparent life stages: the button-shaped juveniles (Figure II-3B, left), in which the calyx does not elevate the crown above the surface but forms a flattened hemisphere attached to the rock, and the fist-shaped adults (Figure II-3B, right), in which the calyx is taller than it is wide and crown height reaches a few centimeters above the surface. The minimum between the two modes lies at about 1.14 cm, which will be used as the dividing line between adult and juvenile specimens for the remainder of the data analysis.

The total area of an image is negatively correlated with the population density (-.041 (individuals m^{-2}) m^{-2}, p=0.0038); that is, closer-range images are likely to appear more densely populated. This is probably because the smallest individuals were invisible in the largest-scale images. The size of individuals was also less variable in areas of denser population (σ^2 of size decreased by 0.0023 cm/(individuals/m^2), p=0.048).

Growth and regeneration rates

The 50th and 99th percentile growth rates among the sample of 60 specimens (or individuals) over the three years sampled were, respectively, 0.044 cm y^{-1} and 0.194 cm y^{-1}. The age estimates for very small, median, and very large specimens (1st, 50th, and 99th percentiles of size) in the sample of 817 measured individuals are given in Table 4. As the errors resulting from this method of measurement are large in proportion to the growth rates, the left tail of the growth rate distribution is below 0, and so no minimum age estimates are given.

When growth rates among the repeatedly-sampled specimens are split by size class, using the value of 1.14 cm derived above from the larger set of body sizes and the average size and growth rate of each individual over all years sampled, growth rates of juvenile and adult size classes differ significantly: adults grow faster than juveniles by a factor of about 2.5. (Individuals ≤1.14 cm: μ=0.026 cm $^{-1}$yr, σ^2=0.069. Individuals >1.14 cm: μ=0.063 cm y^{-1}, σ^2=0.045. Unpaired t-test: difference in means is significant, t=-2.419, p=0.019.) If we take this slower juvenile mean growth rate at face value, we find that an individual would be approximately 44 years old when it reached 1.14 cm. The modal 1.79-cm adult in our sample, after a further 0.65 cm of growth at the adult rate, would then be approximately 59 years old. However, the large variance in the juvenile growth rate suggests that it is near the lower boundary of detection by this method, and is probably not a reliable estimate.

Because our best estimate for the median adult age in our sample is between 40 and 60 years, corresponding to a mortality rate of around 2% per year, we would expect to observe three or four deaths among our sample population of 60 during the 693 days separating the first and last observations. Dead *Holopus* are recognizable as empty calyx stumps, which are common and even abundant in some images. However, no individuals died or disappeared completedly during this time period; the odds of this occurring with uniform 2% per year mortality risk are about 1 in 10, which means that the death rate was lower than expected given the age distribution. Similar reasoning applies to the lack of new individuals: although very young specimens may be unrecognizable in the images, we would expect some three or four individuals to pass into the visible size range and thus appear to be "born" during the ~2 year observation period, but we observed no such instances.

The rate of arm regeneration in the single individual in which it was measured was, on average, 0.6 cm y^{-1} (i.e., 0.00167 cm day^{-1}); this is about ten times the median growth rate and four times the 95th percentile growth rate.

Of all measured adults, 9.8% had visible injuries, an underestimate, as many were photographed with arms closed, obscuring any injuries to the distal arms, as in Figure II-4. Of the 54% that were photographed fully open with all arms visible, 18% exhibited visible injury. Also, large-scale images often did not provide enough detail to identify injury. Accordingly, we use 9.8% as a minimum estimate of adult *Holopus* injury frequency. We observed no arm injuries in juveniles; either injury to such small specimens is rare, or most arms were either in unobservable positions or were too small and unresolved in images.

To estimate the average time between injuries, we follow the equation given in Baumiller (2013 a). The average arm length in adults is approximately 4 cm. We assume that injuries are evenly distributed over the length of the arm, that is, on average half the arm is lost. Then T = ($-t_r$

$\ln(P_{\mathrm{ind}}))^{-1} = (0.00193 \pm .00007\ \mathrm{days}^{-1})^{-1} = 517 \pm 18$ days between injuries. Given the locations of specimens on vertical and overhanging rock faces protected from falling rock debris, we assume that all arm injuries are predation-related.

Discussion

Growth and life history

The age of the average specimen of *H. mikihe* is probably comparable or greater than that of other deep-water stalked crinoids, as given in Table II-1. Using a constant growth rate, the 99% confidence interval gives the median individual's age at 8.7 years, which is lower than that estimated for either *Metacrinus rotundus* or *Endoxocrinus wyvillethompsoni*. However, the 50% confidence interval gives a median age of 39 years, which is substantially older than the age estimates for any of the species in Table II-1. Additionally, these ages do not take into account the different growth rates in adults and juveniles. Regardless of the actual magnitude of the difference between the juvenile and adult growth rates, it is clear that the slower juvenile growth rate means that the age estimates given in Table II-4 are underestimates.

Almost all extant crinoids develop a stalk following a planktonic or brooded larval stage. The feather stars, the majority of order Comatulida, pass through a stalked postlarval stage before taking up a free existence. Taxa that retain a stalk throughout life (e.g., Isocrinida, Hyocrinida, Bourgueticrinidae) do not exhibit a well-defined postlarval stage. Among extant Cyrtocrinida, only members of Holopodidae *(Holopus* and *Cyathidium*) lack a stalk at any known developmental stage, although larvae, which exhibit an internally developing stalk in other crinoid taxa, have not yet been observed in Holopodidae. In this case, juveniles of *Holopus mikihe* are morphologically similar to adults of *Cyathidium* spp, which accords with the general assessment of *Cyathidium* as paedomorphic relative to *Holopus*, although Améziane-Cominardi (1999) notes that tegminal characters of *Cyathidium* are peramorphic. Roux (1976) estimated that the isocrinid *Endoxocrinus wyvillethompsoni* passed through a 2.5 year postlarval juvenile period, based on a large Antarctic comatulid. However, the very slow growth rate documented here for *H. mikihe* indicates that the juvenile period may be much longer, possibly lasting decades.

The observed arm regeneration rate of 0.6 cm y^{-1} is much slower than the extrapolated annual rate of 4.4-4.8 cm y^{-1} estimated for a specimen of the isocrinid *Neocrinus decorus* at similar depths in the Bahamas (Messing et al. 2007) or the initial rate of 6.2 cm $^{-1}$ recorded for aquarium-raised isocrinids, *Metacrinus rotundus*, that had autotomized their entire crown (Amemiya and Oji 1992). However, since the arms of *H. mikihe* are much more robust than those of either isocrinid, the volumetric rate of stereom addition may be more similar.

Crinoids experience predator-related injuries less often in deep water than in shallow water (Oji 1996; Baumiller 2013a). Given the escalating pace of predator-prey relations that has been observed between the Mesozoic and the present by numerous authors (Vermeij 2013), this is consistent with the pattern of migration from onshore to offshore environments over the history of the less-motile clades of modern crinoids (Bottjer and Jablonski 1988; Baumiller et al. 2010). As a result, deep-water assemblages are often "archaic" in appearance, low in modern durophagous predators and dominated by sessile epifaunal suspension feeders (Aronson 1991; Améziane and Roux 1997). The comparatively low injury rates (Table II-2) found here for *H. mikihe* are consistent with their low-intensity deep-water community. The injury rates are lower even than those of some shallow-water Paleozoic crinoid populations, which is remarkable considering the slowness of regrowth in colder temperatures documented in other echinoderms (Davies et al. 1972). Assuming that most mortality in adults is caused by predatory interactions, an average adult age of 50 years means an average "waiting time" of 50 years for a lethal predatory encounter. Since our injury calculation above gave a waiting time of about 1.4 years, this means that about 3% of interactions between *H. mikihe* and its predators are fatal.

The lack of new individuals during the observation period, in combination with the decreased size heterogeneity within more densely populated regions, suggests that recruitment occurs in local bursts either very rarely or sporadically, if not both. The pattern of juveniles growing more slowly than adults is known from other organisms. Trees in dense forests, for example, will remain sapling-sized while waiting for a canopy opening for many years, a pattern described as "advance regeneration" (Messier et al. 1999). This is consistent with the very slow and temporally uneven death rate observed. However, there is no resource whose role is obviously comparable to that of sunlight in a forest canopy, as almost none of the *Holopus* populations appear dense enough to restrict access to current-borne food particles, and no stunting effect of population density was observed. Alternatively, growth rate may be governed purely by current velocity, which regulates food availability. Near the rock surface, currents are slowed by boundary effects; if juveniles are confined within this slow-flowing boundary layer, their food supply may thus simply be insufficient to allow rapid growth until the transition to their adult calyx shape elevates them into more turbulent water. In this case, a rapid change from slower to faster growth could produce the observed local minimum in size frequency around the size where the growth speed transition occurs. It is also likely that different rates or causes of mortality apply to the juvenile and adult size classes; higher mortality in juveniles than in adults would accentuate the size frequency minimum between the two stages.

Habitat and behavior

We observed no consistent current direction at crinoid sites during submersible dives; the trajectories of particles of marine snow indicated that the water moved slowly and changed direction frequently, although we observed apparently tidally induced or influenced flow of up to ~50 cm sec^{-1} and parallel to the local slope in other areas. Therefore, we observed no clear orientation of the oral disc, funnel, bivium, or trivium with respect to the current; instead, the arm funnels of all individuals were oriented normal to the rock face. While this disagrees with preliminary observations published elsewhere, it is not inconsistent with the proposition that unidirectional current flow produces asymmetries (Grimmer and Holland 1990).

It has also been proposed that *Holopus* is a raptorial feeder, capable of contracting its arms very quickly to form a "cage" for large prey items (Grimmer and Holland 1990). However, the individuals observed closing their arms all appear to be responding to water movements generated by the approaching submersible (and not apparently to the submersible's lights) and to do so too slowly to capture at least actively motile organisms. Thus, we infer that such arm closing is a defensive response. Interestingly, a similar function has been inferred for the stem coiling in the Devonian flexible crinoid *Ammonicrinus*, associated with a separate origin of muscles (Gorzelak, Głuchowski, and Salamon 2014). Moreover, the individuals observed with semi-closed arms do not appear to be in a cage-like position; instead, the center of the calyx's oral surface is exposed and the arms are distally enrolled (Figure II-4). Anatomical comparisons to other raptorially-feeding echinoderms, specifically the gorgonocephalid basket stars *Gorgonocephalus caputmedusae* (Emson, Mladenov, and Barrow 1991; Rosenberg et al. 2005) and *Astrophyton muricatum* (Macurda 1976), support these inferences: no food-capturing hooks or similar articulated adambulacral structures have ever been described for any holopodid (Donovan 1992). On this basis, we find no evidence in favor of the raptorial-feeding hypothesis.

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Figures

Figure II-1. Spindle diagram of cyrtocrinid generic diversity through time. (A) all cyrtocrinids, (B) all cyrtocrinids by superfamily. Vertical distance is proportional to time, with the height of the Holocene exaggerated by a factor of two for visibility; horizontal distance indicates generic diversity of the cyrtocrinids during each ICS stage. Genus origin and extinction times are taken from the Treatise on Invertebrate Paleontology (Hess, Messing, and Ausich 2011). A more recent report of *Hemicrinus* from the Paleocene is also included (Salamon and Gorzelak 2011). Extension into the Triassic, indicated by asterisk in (A), is based on ossicles of cyrtocrinid affinity reported from the Rhaetian (Salamon, Gorzelak, and Zatoń 2009) and undescribed specimens from the Carnian reportedly resembling cyrtocrinids (Hess 2006; Salamon, Gorzelak, and Zatoń 2009). This material has not been identified to the superfamily level and is therefore not included in (B).

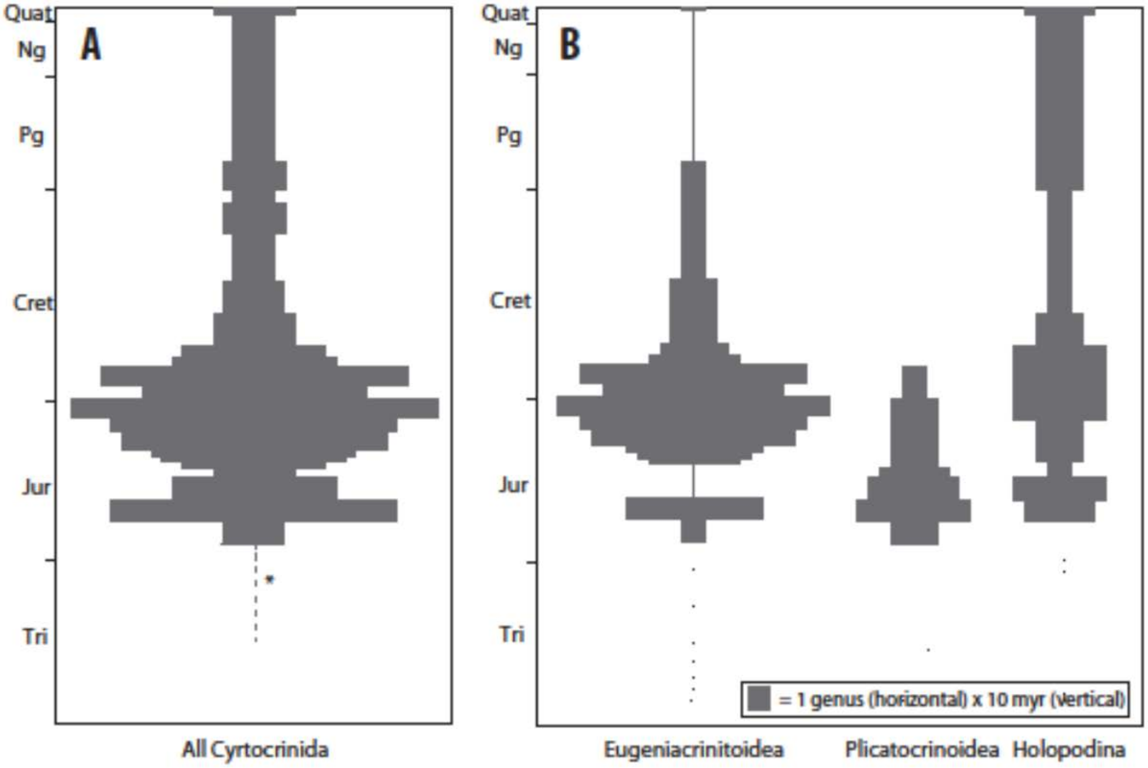

Figure II-2. (A) Measurement of *Holopus* calyx size at widest point of calyx, demonstrated on a dead preserved individual. (B) Example of parallel lasers (green dots) used for size measurement of living specimens. (C) Individual with regrowing arms used in the calculation of arm regrowth rate and photographed in all three years. Note complete absence of radials in 2012. Photographs by C. G. Messing and T. K. Baumiller.

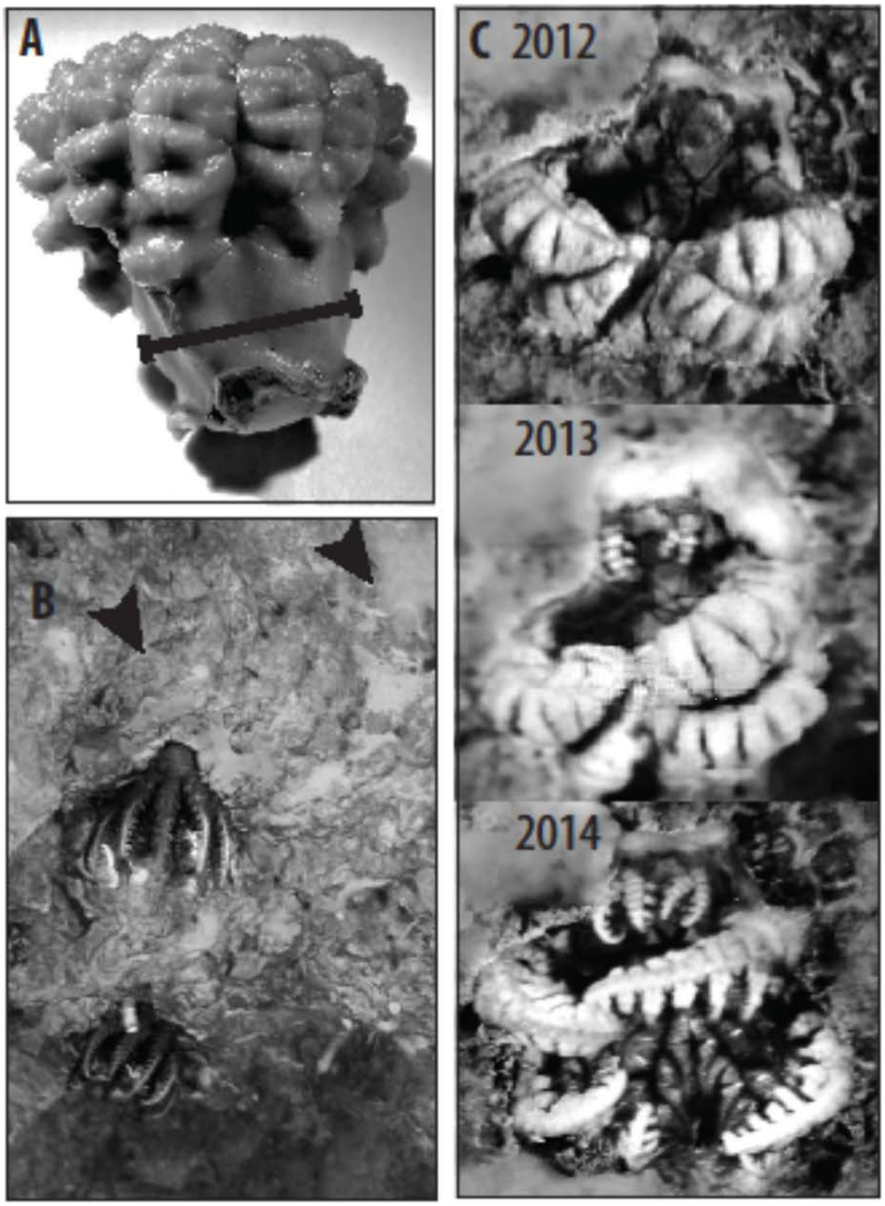

Figure II-3. (A) Size histogram and probability density curve (calculated by kernel density estimation) for all 817 individuals, showing bimodal size distribution. Based on the density curve, “juvenile” size mode is at 0.84 cm, “adult” at 1.79 cm, and the minimum between them is 1.14 cm. (B) Example “juvenile” (top left) and “adult” individuals of *H. mikihe*, along with a large *Cyathidium* (dark bluish with coiled arms) at upper right. White rings on substrate are bases of dead individuals, usually of indeterminate genus. Note similarity of calyx shape in juvenile *Holopus* and adult *Cyathidium*. Photograph by C. G. Messing.

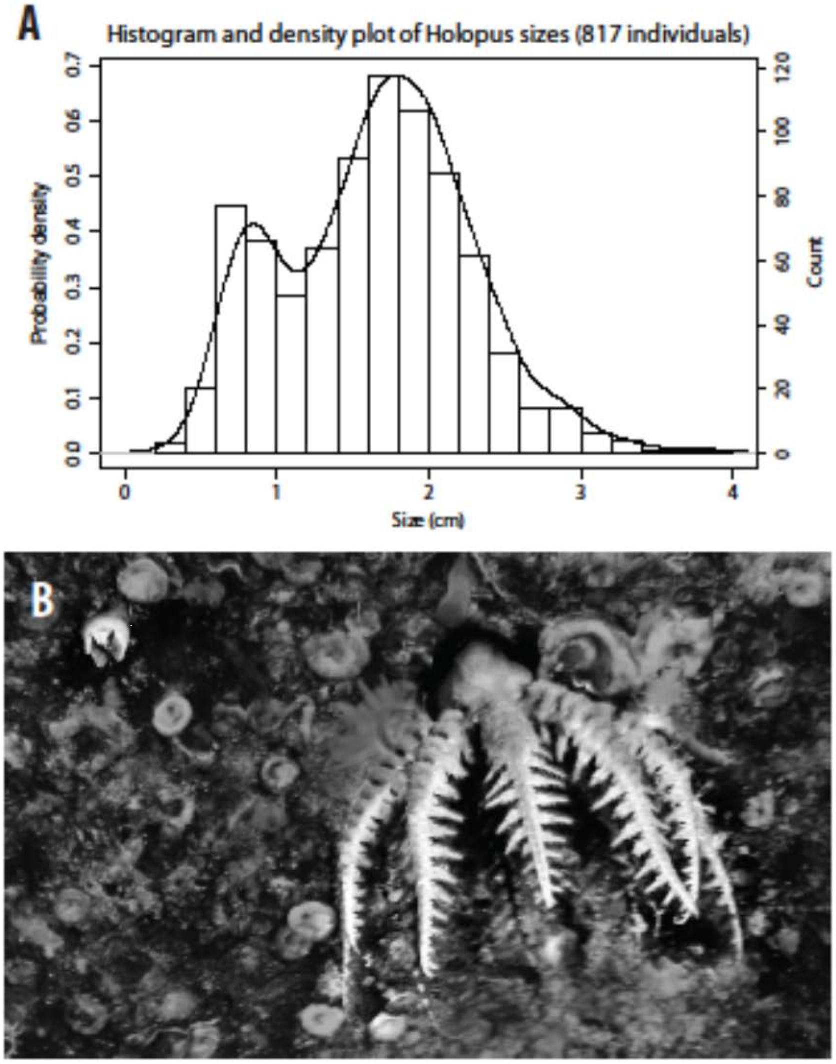

Figure II-4. Different arm positions in adult *H. mikihe*: fully open (bottom right), mostly open with distal arm tips curled (top left), partially closed (bottom left), almost completely closed (right center). Figure II-1A shows an example of the fully closed position (in a dead individual). These partially-closed postures would protect the distal arm tips and permit relatively quick movement to a fully closed position, while still allowing some food collection. Photograph by C. G. Messing.

Tables

Table II-1. Estimated age ranges for extant stalked crinoids.

Taxon	Depth (m)	Mean age (y)	Max age (y)	Reference
Metacrinus rotundus	100 - 200	10		(Oji 1989)
Cenocrinus asterius	215		>20	(Messing et al. 2007)
Endoxocrinus wyvillethompsoni	1420 - 2615	15	>20	(Roux 1976)
Bathycrinus carpenteri	1420 - 2615		10-15	(Duco and Roux 1981)
Holopus mikihe	430 - 640	39	73	This study

Table II-2. Comparisons of injury frequency among different crinoids and other echinoderms.

Taxon	Time	Individuals injured	Arms injured	Frequency (days)	Reference
Endoxocrinus	Modern	71%	16-61%		(Oji 1996)
Florometra serratissima	Modern	80%	27%		(Mladenov 1983)
Florometra serratissima	Modern	18%	1-18%	650 - 850	(Baumiller 2013a; Baumiller 2013b)
Cenometra bella	Modern	100%	29%	8 - 12	(Baumiller and Gahn 2013)
Eugeniacrinites cariophilites	Jurassic	~10% (cup only)			(Hess 2014)
Pilocrinus moussoni	Jurassic	8.3% (cup only)			(Hess 2014)
Rhodocrinites kirbyi	Mississippian	26%	8%	30 - 42	(Baumiller and Gahn 2013)
Le Grand crinoid fauna	Mississippian	9%			(Gahn and Baumiller 2005)
Paleozoic crinoids	Devonian - Pennsylvanian	12%			(Baumiller and Gahn 2004)
All echinoderms	Modern	21-72%			(Lindsay 2010)
Holopus mikihe	Modern	9.8%	2%	497 - 538	This study

Table II-3. Crinoid species identified in submersible trips off Roatán, Honduras, between 2012 and 2014.

Order	Family	Species/subspecies
ISOCRINIDA	Isselicrinidae	*Cenocrinus asterius*
		Endoxocrinus parrae carolinae
COMATULIDA	Comatulidae (formerly Comasteridae)	*Comactinia meridionalis hartlaubi* *Davidaster discoideus*
		Neocomatella pulchella
	Charitometridae	*Crinometra brevipinna*
	Bourgueticrinidae	*Democrinus* sp.
	Atelecrinidae	unidentified genus and species
CYRTOCRINIDA	Holopodidae	*Holopus mikihe*
		Cyathidium pourtalesi

Table II-4. Age estimates for *Holopus mikihe* individuals of 1st, 50th, and 99th percentile sizes, based on 50th and 99th percentile growth rates.

Size		Age (years), by growth rate percentile	
Percentile	Measurement (cm)	50th (0.044 cm/yr)	99th (0.194 cm/yr)
1st (smallest)	0.52	12.0	2.7
50th (median)	1.70	38.9	8.7
99th (largest)	3.12	71.5	16.1

Chapter III.
Temporal trends of predation resistance in Paleozoic crinoid arm branching morphologies

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Abstract

The rise of durophagous predators during the Paleozoic represents an ecological constraint imposed on sessile marine fauna. In crinoids, it has been suggested that increasing predation pressure drove the spread of adaptations against predation. Damage to a crinoid's arms from nonlethal predation varies as a function of arm branching pattern. Here, using a metric for resilience to predation ("expected arm loss," EAL), we test the hypothesis that the increase in predation led to more predation-resistant arm branching patterns (lower EAL) among Paleozoic crinoids. EAL was computed for 230 genera of Paleozoic crinoids and analyzed with respect to taxonomy and temporal and geographic range. The results show significant variability among taxa. Camerates, especially monobathrids, display a pattern of increasingly convergent and predation-resistant arm morphologies from the Ordovician through the Devonian, with no significant change during the Mississippian. In contrast, the mean EAL among cladids follows no overall trend through the Paleozoic. Regenerating arms are known to be significantly more common in camerates than in other Paleozoic taxa; if regeneration is

taken as a proxy for nonlethal interactions with durophagous predators, this indicates that nonlethal predation occurred more often among camerates throughout the Early and Middle Paleozoic. In addition, frequency of injury among camerates is inversely correlated with EAL and positively correlated with infestation by parasitic snails. From this we conclude that decreasing EAL signals a selective pressure in favor of resistance to grazing predation in camerates but not in other subclasses before the Mississippian, with an apparent relaxation in this constraint after the late Devonian extinctions.

Introduction and Background

Stalked crinoids live an exposed and primarily sessile lifestyle, vulnerable to predators. However, their regenerative capacities mean that they can recover from most damage that is not fatal. Such nonlethal predation is thought to be frequent in modern crinoids as inferred from both truncated arms and absent or regenerating visceral masses, and predators have been observed carrying away arms (Mladenov 1983; Meyer et al. 1984; Meyer 1985; Schneider 1988; Nichols 1994). Although there are other potential sources of arm loss resulting in regrowth, including abiotic trauma, physiological stress, and normal ontogeny, most damage in modern crinoids is thought to result from biotic interactions (Mladenov 1983; Meyer 1985; Lawrence and Vasquez 1996). In Paleozoic crinoids, the existence of nonlethal predation is attested by the presence of regenerating arms in fossil specimens (Oji 2001; Baumiller and Gahn 2004; Gahn and Baumiller 2005), and the identity of predators is suggested by placoderm-like bite marks (Gorzelak et al. 2011).

A wide variety of features in crinoids have been described as possible adaptations to predation. These include (1) behavioral and mobility-related adaptations, such as nocturnal activity, semicryptic habit, swimming and crawling (Meyer and Macurda 1977; Vermeij 1977), and deep habitat (Bottjer and Jablonski 1988); (2) biochemical defenses, such as unpalatability (Rideout et al. 1979; McClintock et al. 1999) and aposematic coloration (Lawrence 2009); (3) physical defenses such as thick or spiny calycal plates (Signor and Brett 1984) or dense spiny pinnules proximal to the oral surface (Meyer 1985); and (4) optimizations such as locating the gonads far away from potentially fatal areas (Lane 1984), ontogenetic loss or autotomy of the stalk (Baumiller 2008; Baumiller et al. 2008; Janevski and Baumiller 2010), and autotomy and autotomy-related optimizations of the arms (Oji and Okamoto 1994). The last of these is the focus of the work presented herein.

Although most studies of functional morphology in crinoid arms have tended to focus on improvement of feeding ability (Cowen 1981; Kammer and Ausich 1987; Baumiller 1993; Brower 2006), Oji and Okamoto (1994) observed that there are arm branching patterns that reduce the damage sustained when arms are lost, which may not necessarily coincide with optimal feeding strategies. They described two optima in the space of possible arm forms, given that the loss of even a portion of a food-gathering appendage is detrimental to the organism even if it can regenerate, which they called the "harvesting" and "anti-predation" paradigms. In the former, for a certain total length of arms in a symmetrical, planar organism, food gathering efficiency is thought to be maximized when the branches are spaced uniformly throughout the crown; in the latter, arms branch very close to the base so as to minimize loss when the arm is autotomized as near as possible to the point of injury. Among post-Paleozoic crinoids, they found that anti-predatory morphologies have increased in frequency since the Jurassic to near universality among modern crinoids; this, they suggest, represents an adaptation to post-Paleozoic predators.

Although specialized arm autotomy articulations (syzygies/cryptosyzygies) may not have been present in Paleozoic crinoids (Oji 2001), the same morphological optimizations apply to arm loss via predator attack. The frequency of regenerating arms has been found to change over the Paleozoic (Baumiller and Gahn 2004), suggesting that predation pressure leading to arm loss may have varied also. Changes in the diversity and composition of predators in the Paleozoic have also been recognized. For example, the Devonian has been identified as a time of intensified durophagous predation (Signor and Brett 1984; Bambach 1999; Dahl 2010), and more recently the end-Devonian Hangenberg extinction was recognized as a period of high turnover among predatory fishes (Sallan and Coates 2010). If some of these changes affected the intensity of nonlethal predation on crinoids, changes in the frequencies of more predation-resistant arm morphologies would be expected. We therefore chose to explore how crinoid arm morphologies changed during the Paleozoic, specifically focusing on changes in frequency of morphologies resistant to partial predation.

Materials and Methods

Expected Arm Loss

In order to quantify morphological resistance to nonlethal predation, we used the "expected arm loss" metric of Oji and Okamoto (1994). As described above and discussed in detail in that paper, the arm branching morphologies of crinoids are not all equivalent in terms of the proportion of arm loss during a nonlethal encounter with a predator: some branching morphologies result in a smaller proportion of arm loss during an encounter than do others. Their model makes the following assumptions: (1) individuals are pentaradially symmetrical; (2) all nonlethal attacks have an equal probability of severing the arm at any point along its length; and (3) the arm is lost completely above the point of attack and unaffected below it. An arm, for these purposes, is defined as all brachials proceeding from a single radial; the expected arm loss can therefore be compared across taxa without regard for the number of free arms, because all individuals in the sample have five radials.

We omit from our analysis all genera for which the first assumption does not hold. The second assumption is a simplification, but one that can be easily relaxed. An equal probability model is most neutral, as it assumes no knowledge of the predator's preferences; however, if attacks are known to be concentrated on any specific part of the arm, the model can accommodate such alternative distributions of probability. Most conditions that would violate this assumption would lead to the expectation of the arms being severed closer to the base, and the effect on EAL of branching closer to the base is therefore increased. For instance, predators eating the crinoid's arms might preferentially bite off arms near their bases; or if predators were targeting parasites, the probability of attack would be elevated at the locations preferred by the parasites, which we might expect to be located near the mouth for purposes of stealing food or excreta. Our assumption that the probability of injury is uniform along the arm length is therefore a conservative one. The third assumption is likely to be valid because most Paleozoic crinoids had undifferentiated arm articulations. Only among a few, the advanced cladids and some camerates, were the most proximal articulations different from all others, and even among those taxa none have been recognized with the specialized articulations for autotomy characteristic of modern crinoids (Oji 2001), although the phenomenon has not been fully explored. Thus, whereas in modern crinoids failure occurs at these specialized articulations, in Paleozoic crinoids we assume that it would occur directly at the damaged articulation, because there was no preferred place of failure.

Given the above assumptions, expected arm loss (EAL) is defined as the expected value for the proportion of a single arm lost in any single attack from a predator:

$$EAL = \sum_{brachitaxes} (\text{proportional length of segment } i)(\text{proportional length above segment } i)$$

This gives an estimate of how susceptible the animal is to such damage. Lower EAL indicates more predator-resistant morphology.

As an example, consider a crinoid with five simple bifurcating arms that divide halfway up their length, as illustrated in Figure III-1A. We will illustrate the computation of EAL for one arm of this crinoid step by step.

1. First, consider an injury that occurs on one of the two free arm segments, above the node (the branching point). This segment makes up 1/3 of the total arm length, which given assumption 2 (evenly-distributed probability of attack) means that the probability of injury on that segment is 1/3. Given assumptions 2 and 3, on average such an injury would result in the loss of 1/2 of that segment. Thus an injury on one of the

two free arm segments results in the expected arm loss of $\left(\frac{1}{3} * \frac{1}{2}\right) = \frac{1}{6}$ of the total arm length.

2. Second, consider an injury that occurs below the node, on the lower segment. The probability that this segment will be injured is $\frac{1}{3}$, equal to that of the other two segments, because they are all of equal length. However, a strike below the node leads to the loss both of $\frac{1}{2}$ of the lower segment ($\frac{1}{6}$ of total arm length) and of the two segments above the node ($\frac{2}{3}$ of total arm length), in total $\frac{5}{6}$ of arm length.
3. To calculate EAL for this arm branching pattern, we add up the expected losses for an injury on each segment; i.e., for the upper left segment $\left(\frac{1}{3} * \frac{1}{6}\right)$, for the upper right segment $\left(\frac{1}{3} * \frac{1}{6}\right)$, and for the lower segment $\left(\frac{1}{3} * \frac{5}{6}\right)$. The EAL for this branching style is therefore $\frac{7}{18}$: $2\left(\frac{1}{3} * \frac{1}{6}\right) + 1\left(\frac{1}{3} * \frac{5}{6}\right)$.

For comparison, an arm that bifurcates once at the base (Fig. 1B) has an EAL of $2\left(\frac{1}{2} * \frac{1}{4}\right) = \frac{1}{4}$; bifurcating twice at the base (Fig. 1C) halves that to $4\left(\frac{1}{4} * \frac{1}{8}\right) = \frac{1}{8}$. The computation of EAL for real crinoids, such as a typical camerate (Fig. 1D) and a typical cladid (Fig. 1E), is the same.

For a uniform distribution of injury probability over length, the value of EAL varies from ~0 to 0.5. In general, EAL decreases (indicating less vulnerability to predation) when the number of free arms is increased or when they branch closer to the base, as shown in Figure III-2.

Data

In order to characterize changes in the prevalence of predation-resistant morphology, we measured the arms and calculated the EAL for crinoid genera ranging across the Paleozoic. Individual specimens were chosen for the presence of at least one arm structure reasonably complete and consistent with the genus description, and for presence in Webster's compendium of Paleozoic crinoid genera (Webster 2003). The final sample included a total of 229 genera; of these, there were 74 Camerata and 139 Cladida, with the remaining 34 distributed among the Flexibilia and Disparida. Names and EAL for all genera in this study, with origin and extinction dates taken from Webster (2003), can be found in Appendix A.

A total of 198 of the 230 genera were measured from plates in Volume T of the Treatise on Invertebrate Paleontology (Moore et al. 1978). An additional 32 photographs and 31 physical specimens from the private collection of Joseph M. Koniecki (www.crinus.info) were measured to give estimates of within-genus variability, fill in the intervals for which few good specimens were available in the Treatise, and assess possible biases due to the flattening of arm structures to two-dimensional images. Photographs and plates were measured using Adobe Illustrator; real specimens were measured using a flexible wire and a ruler. Data were recorded in a format that preserved the length, relationship, and state of preservation of all brachitaxes. Brachials incorporated in the calyx were recorded as zero length. The EAL for each genus was calculated from the measured arm structure as described above. These data are given in Appendix A.

We tested for biases introduced by the use of plates and photographs instead of physical specimens, preservation quality, specimen size, and inconsistency between different collections. Results of tests for bias are given in Table 1. There was no significant difference between measurements of EAL obtained from TIP plates and those from modern photographs of the private collection, nor was there a significant difference between measurements obtained from those photographs and the physical specimens themselves. We concluded that EAL is robust to differences between collections and that no significant bias exists in measurements taken from photographs or plates relative to actual specimens. The difference between specimens with intact arms and those in which the longest free arm was broken was borderline-significant, but the magnitude of the effect was small. Within the final total of 229 genera, our sampling is reasonably reflective of overall Paleozoic crinoid generic diversity as described by Webster (2003); for each time bin, about one-quarter of the genera in that database are present in our sample ($\mu = 0.26$, $\sigma^2 = 0.08$). For further information on sampling, see Appendix B.

In order to determine the robustness of the EAL measure, we calculated standard errors for single-species and single-genus collections. The single-species data comprise multiple examples of all five rays from specimens of the camerate *Amphoracrinus viminalis*, whose arm branching is described as "highly variable," from the early Tournasian Meadville Shale of Ohio (Ausich and Roeser 2012: p. 492). A bootstrap analysis of the *A. viminalis* data was conducted by calculating the EAL for each figured ray, recombining them 1000 times into "individuals" with five rays each, and taking the mean EAL for each of them. Standard error for these data was 0.005; because *A. viminalis* has unusually high variability in arm branching, this is probably near the upper limit for within-species variation. Bootstrap standard error for single-genus collections of *Arthroacantha* (ten specimens) and the cladid *Cupulocrinus* (28 specimens) taken from Mr. Koniecki's private collection were, respectively, 0.008 and 0.005, as compared to mean within-time-bin standard deviations of 0.05 and 0.1 for camerates and cladids, respectively. We conclude that within-species and within-genus EAL variability is low compared to differences between genera. The standard error for all genus EAL values in the data set was set to 0.006, the mean of *Arthroacantha* and *Cupulocrinus*. The values were grouped into time bins, and means of all genera present within each bin were tested for statistically significant correlation with time.

Results

Our results are summarized in Figure III-3. There is no significant temporal trend in mean EAL for all crinoids over the Paleozoic, as shown in Figure III-3A. However, when the two largest Paleozoic crinoid clades, camerates and cladids, were analyzed separately (Fig. III-3B), a strikingly different pattern emerged: mean camerate EAL exhibits a significant downward trend over the Paleozoic, while the cladids show no net trend. The significant decrease in camerate EAL is not strictly monotonic; the steep decrease in the early to mid Paleozoic is followed by an interval of low, but stable, EAL in later Paleozoic. As discussed above, EAL is governed by two properties of the arm: the number of free arms and the height at which they branch (Fig. 2). Time-bin means of EAL and number of free arms in camerates show no significant correlation ($p = 0.2$), leading us to conclude that the aforementioned decrease in camerate EAL occurred via an increase in the number of camerate taxa with arms branching proximal to the calyx, rather than an increase in the number of free arms.

Qualitatively, these patterns are robust with regard to bin size and evenness (see Appendix B). The Spearman rank-order correlations whose p-values are given in Table 2 were calculated using the ICS epoch time bins, but they do not change significantly when different bin sizes are used. All show a consistently decreasing value of EAL among camerates and fluctuating values of EAL among cladids during the Paleozoic.

Discussion

We have argued that a lower EAL is more adaptive in situations where nonlethal predators represent a substantial burden on crinoids. Our results indicate that EAL declined significantly in one major crinoid clade, the camerates, but not in the other, the cladids. If our adaptive hypothesis is correct, we would expect nonlethal predation pressure to be higher for camerates than for non-camerates. To test this, we need an independent measure of predation pressure.

Nonlethal predation intensity on crinoids has generally been estimated from the frequency of injured individuals (e.g. Meyer 1985; Schneider 1988). Baumiller and Gahn (Baumiller and Gahn 2004; Gahn and Baumiller 2010) extended this approach to Paleozoic crinoids by counting the proportion of injured and regenerating crinoids in numerous Lagerstätten from the Ordovician through Pennsylvanian; these data are given in Figure III-4 and Table III-3. Camerates, the dominant group in their samples, were found to be regenerating significantly more often than expected (binomial $p < 0.01$). Cladids, the second most abundant taxon, were injured significantly less often than expected (binomial $p < 0.01$). When compared directly, frequency of injured camerates is significantly higher than that of injured cladids (χ^2 $p < 0.0001$). Additionally, in each period from the Ordovician through the Mississippian for which Baumiller and Gahn (2004) were able to gather data on camerate injuries, (1) the incidence was from 2.5 to 12 times higher than among non-camerates, and (2) the temporal trend in injury frequencies exhibits a significant ($\rho = -0.8$, $p = 0.005$) correlation with EAL, as shown in Figure III-5. Thus, if frequencies of injuries are accepted as a proxy for predation, these results suggest that camerates were under heavier predation pressure than expected and significantly greater pressure than cladids. (Injuries to disparids, the third most abundant taxon, were also significantly lower than expected.)

In order to use the number of visibly injured and regenerating individuals as a proxy for intensity of partial predation, following Gahn and Baumiller (2004, 2005, 2010), we must make two assumptions: (1) a consistent proportional regeneration rate across the taxa being compared, and (2) a very low ratio of fatal to nonfatal injuries. If both of these assumptions hold, then the number of individuals with visibly regenerating arms accurately reflects the rate of injury, and therefore the rate of predator-prey interactions. For a more complete discussion of this problem, see Baumiller (2013). Additionally, the number of free arms might conceivably have an influence on either injury frequency or regeneration rate. For those genera present in both this data set and that of Baumiller and Gahn (2004), though, we find no correlation ($p > 0.4$) between the number of free arms and the proportion of individuals regenerating at least one arm.

These results on arm regeneration frequencies correspond to what one would expect if nonlethal predation were the factor driving the evolutionary response of camerate arms. We suggest that the changes in arm branching morphology were indeed driven by predator pressure that was selectively greater on camerates, and that lower EAL is an anti-predatory adaptation in early Paleozoic camerates, just as in Mesozoic crinoids. We conclude that the changes in arm branching morphology were indeed driven by predator pressure that was selectively greater on camerates, and that lower EAL is an anti-predatory adaptation in early Paleozoic camerates, just as in Mesozoic crinoids.

Ecological correlates of predation

If, as we have suggested here, camerate trends in arm branching morphologies leading to lower values of EAL were a consequence of significantly higher frequencies of injuries, we are left with the question of why this would be true for camerates and not other crinoids. One possibility is that predation pressure was constant on all crinoids, but camerates suffered lower mortalities, i.e., were better able to survive predatory attacks. At present we have no data to evaluate this hypothesis; no morphological, physiological, or behavioral features are known or suspected to make camerates more resilient. An alternative explanation is that grazing pressure was higher on camerates. Grazing predation on epibionts has been hypothesized as an explanation for why modern fish have been observed to bite off arms of crinoids and spit them out: the predators' main targets could be the numerous and diverse parasites, commensals, and epibionts instead of the crinoids' distasteful arms (Meyer 1985; Brett 2003; Baumiller 2008). The extreme cryptic coloration of many of these epibionts, camouflaging them against the crinoids' often vivid coloration, further suggests that they are subject to selection from visual predators such as fish (Hempson and Griffiths 2008). Were crinoid epibionts the targets of Paleozoic predators and, if so, why would camerates experience greater intensity of this type of interaction?

A possible answer is offered by the finding that parasitic platyceratid snails prefer camerate hosts (Gahn and Baumiller 2006). Platyceratid infestation occurs overwhelmingly in camerates, and their frequency declines along with that of camerates during the late Paleozoic, although their preference is not sensitive to time or correlated to EAL; see Figure III-5 and Table III-4. The presence of parasitic platyceratids, which position themselves on the oral surface of the calyx, might draw the attention of predators, perhaps resulting in incidental damage to the arms (Brett and Walker 2002; Brett 2003; Brett et al. 2004).

In order to investigate this further, we reanalyzed data from the Paleozoic Lagerstätte reported by Gahn and Baumiller (Baumiller and Gahn 2004; Gahn and Baumiller 2005, 2006). All crinoid genera from those studies were categorized as platyceratid hosts or not; as injured (with regenerating arms) or uninjured; and as camerates, cladids, disparids, or flexibles. A chi-squared test for the taxonomic preference of infestation among the genera reported by Baumiller and Gahn (2004), given in Table III-3, shows that camerate genera are significantly ($p < 0.001$) more likely to be infested than non-camerates and cladids ($p < 0.05$). Injuries are significantly more common in genera known to be hosts than in genera that have not been recognized as hosts (Table III-4), regardless of whether one counts genera ($p < 0.01$) or individual specimens belonging to a given genus ($p < 0.001$). This is consistent with the hypothesis of platyceratid targeting (Brett 2003), though it is also possible that parasites and predators both targeted the same camerate taxa for another reason, such as food-gathering ability.

The downward trend in camerate EAL reaches its minimum in the Late Devonian, after which camerates show little change in EAL. This may be due to a natural minimum value to the adaptation: the Devonian forms with the lowest values of EAL have many free arms that branch at the base, and further reduction in EAL could be achieved only by adding more arms. It is possible that there is some maximum number of arms past which crowding reduces filtering capacity, or that multiple closely packed adjacent arms can be bitten off by a predator all at once, obviating the advantage of having more.

Alternatively, an ecological change, such as an extinction, may have altered the selective pressure imposed by predators. It has been postulated that the taxonomic turnover among fishes during the Hangenberg extinction led to a change in the dominant mode of durophagous predation. The dominant Devonian durophagous fishes, placoderms, and arthrodires, which went extinct at that time, were primarily shearing predators; the Mississippian chondrichthyans and actinopterygians that replaced them were generally crushing predators (Sallan and Coates 2010). Corroborating this, angular shell fragments of the type produced by crushing predation became more common after the Hangenberg extinction (Salamon et al. 2013). Sallan et al. (2011) additionally conclude that the Tournaisian–

Visean peak in crinoid diversity was a reaction among camerates to the disappearance of Devonian predatory fish during the end-Devonian Hangenberg extinction.

If the dominant mode of predation changed from nonlethal grazing to crushing at this time, then the higher EAL in camerates originating in the Tournaisian may have been a response to the relaxation of selective pressure from that form of predation. Anti-predatory crinoid arm morphologies are likely to have been less effective against crushing predators, and as these predators became dominant after the Devonian, crinoids might have responded to them instead; a peak in camerate spinosity in the Mississippian (Signor and Brett 1984) and a driven trend in monobathrid camerates toward a decreasing variety and number of ossicles in the calyx during the end-Devonian extinction (Simpson 2010) can both be interpreted as specifically anti-crushing defenses.

Conclusions

Arm morphologies well adapted to surviving frequent arm loss became increasingly common in camerate crinoids during the Paleozoic. However, cladids, the second largest taxon, did not exhibit a similar trend. A plausible explanation for these contrasting patterns is that predation leading to arm loss was greater on camerates than cladids, consistent with evidence that the frequency of arm loss and regeneration both was higher in camerates and increased in camerates during this period (Baumiller and Gahn 2004; Gahn and Baumiller 2010).

A possible reason for the taxonomic difference in adaptation to predation is the observed preference of platyceratid snails for camerates, and for particular taxa of camerates (Ausich 1980; Baumiller and Gahn 2004; Gahn and Baumiller 2006). If these gastropods, and perhaps other crinoid infesters, were the primary targets of predators (Meyer 1985; Brett 2003; Hempson and Griffiths 2008), it could incur incidental damage to their hosts and provide selective pressure toward predator-resistant arm morphologies.

The camerate EAL values plateau by the Middle Devonian, corresponding possibly to a natural minimum in the adaptive value of arm patterns and possibly to an ecological shift in predator strategy. A shift in predatory strategies on crinoids is likely given the post-Devonian change in dominance of predatory fishes that made anti-grazing adaptations less effective and instead favored anti-crushing adaptations (Signor and Brett 1984; Waters and Maples 1991; Sallan and Coates 2010; Simpson 2010; Sallan et al. 2011).

Acknowledgments

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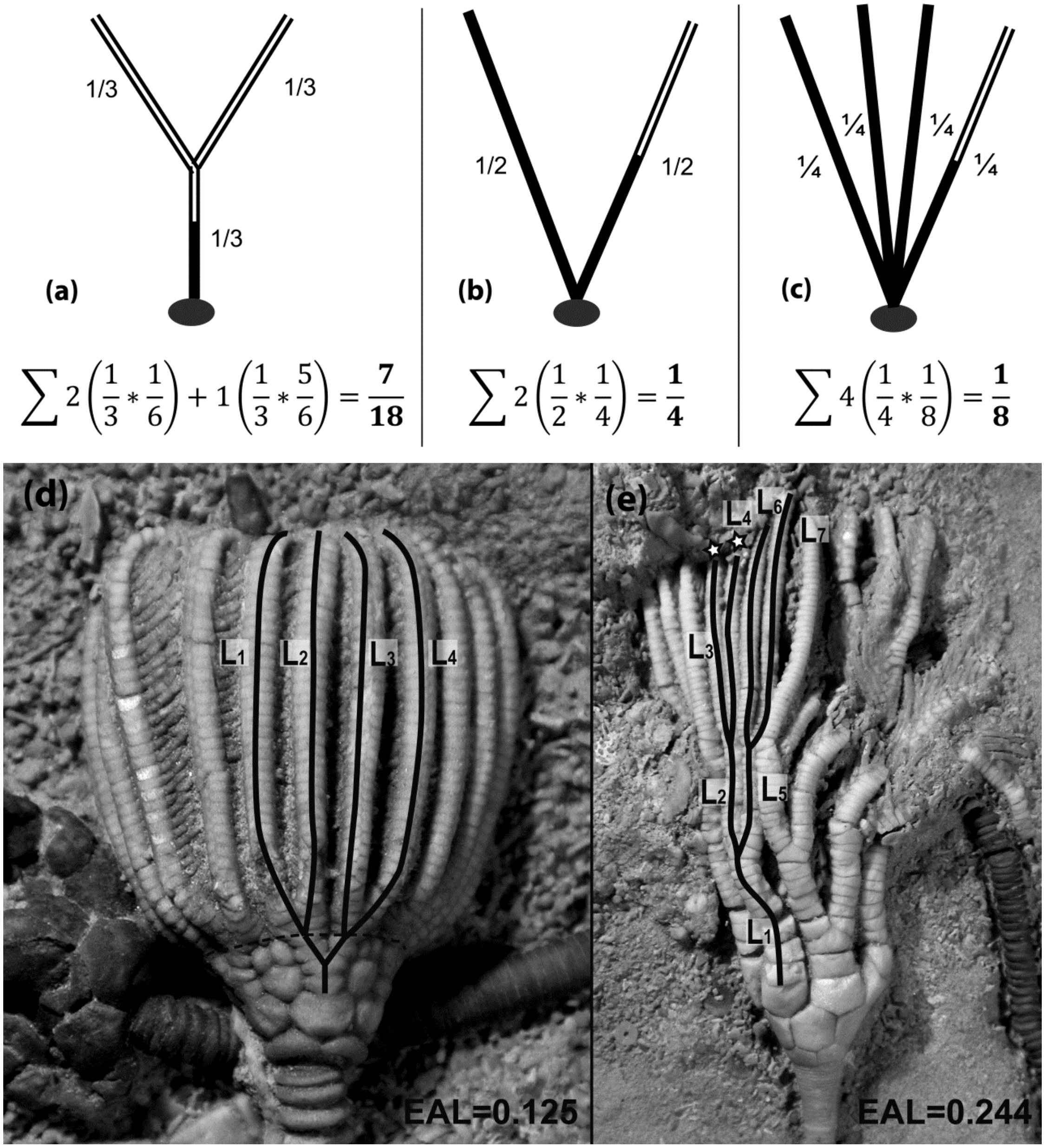
Figures

Figure III-1. Measurements and calculation of expected arm loss (EAL). A–C, Three simplified crinoid arms. If the animal in A is attacked by a predator that bites off a single arm at a random point, for each of the three segments the probability of the injury occurring on that segment is $\frac{1}{3}$. If the injury occurs on one of the two free arm segments, the arm loses on average $\frac{1}{6}$ of its length; if it occurs on the lower segment, it loses $\frac{5}{6}$ of its length. The EAL is the sum over all segments: $2\left(\frac{1}{3} * \frac{1}{6}\right) + 1\left(\frac{1}{3} * \frac{5}{6}\right) = \mathbf{\frac{7}{18}}$ = 0.39. By the same reasoning the arm in B has half its length in each segment and two segments, for an EAL of 0.25, and that in C has an EAL of 0.125. D, E, Photographs and calculations for two typical specimens. D, *Abatocrinus* (a camerate). Brachials incorporated in cup, indicated by dashed line, are counted as zero length, so $EAL = \frac{\left(L_1 * \frac{L_1}{2}\right) + \left(L_2 * \frac{L_2}{2}\right) + \left(L_3 * \frac{L_3}{2}\right) + \left(L_4 * \frac{L_4}{2}\right)}{L_1 + L_2 + L_3 + L_4}$. E, *Blothrocrinus* (a cladid). Stars indicate broken free arms.

$$EAL = \frac{\left(L_1 * \left(\frac{L_1}{2} + L_2 + L_3 + L_4 + L_5 + L_6 + L_7\right)\right) + \left(L_2 * \left(\frac{L_2}{2} + L_3 + L_4\right)\right) + \left(L_3 * \frac{L_3}{2}\right) + \left(L_4 * \frac{L_4}{2}\right) + \left(L_5 * \left(\frac{L_5}{2} + L_6 + L_7\right)\right) + \left(L_6 * \frac{L_6}{2}\right) + \left(L_7 * \frac{L_7}{2}\right)}{L_1 + L_2 + L_3 + L_4 + L_5 + L_6 + L_7}$$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$\sum 2\left(\frac{1}{2}*\frac{1}{4}\right)=\mathbf{\frac{1}{4}}$
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(d)
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L_2
L_3
L_4
EAL=0.125
(e)
L_4
L_6
L_7
L_3
L_2
L_5
L_1
EAL=0.244

Figure III-2. EAL as a function of node location for different numbers of free arms. The number of free arms and the locations at which they branch govern the EAL value for a given arm; the minimum value is therefore infinitesimal and the maximum is 0.5. Note that EAL decreases as the number of free arms increases and as nodes shift toward the base.

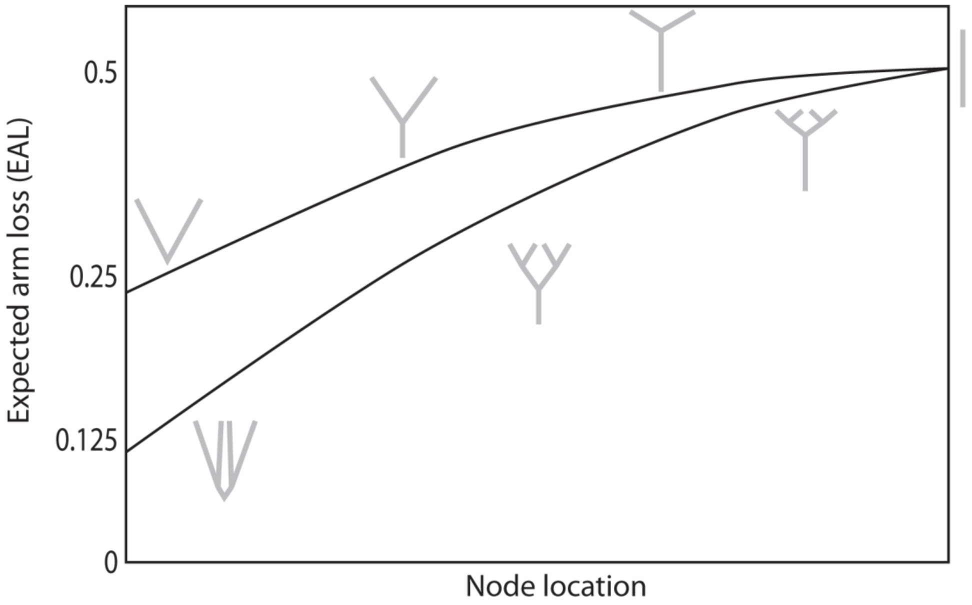


Figure III-3. Mean EAL values by time; lower values indicate more predator-resistant morphologies. A, All genera in sample. Numbers along bottom axis indicate sample size in time bin. B, Genera split by subclass. Numbers at top and bottom indicate respectively the number of cladids and the number of camerates in each bin. Error bars indicate 1 bootstrapped standard deviation. Note that cladid and camerate values diverge by the Devonian. Neither the whole sample nor the cladid subsample displays a clear trend over time, whereas camerate EAL decreases up to the late Devonian and stays uniformly low thereafter.

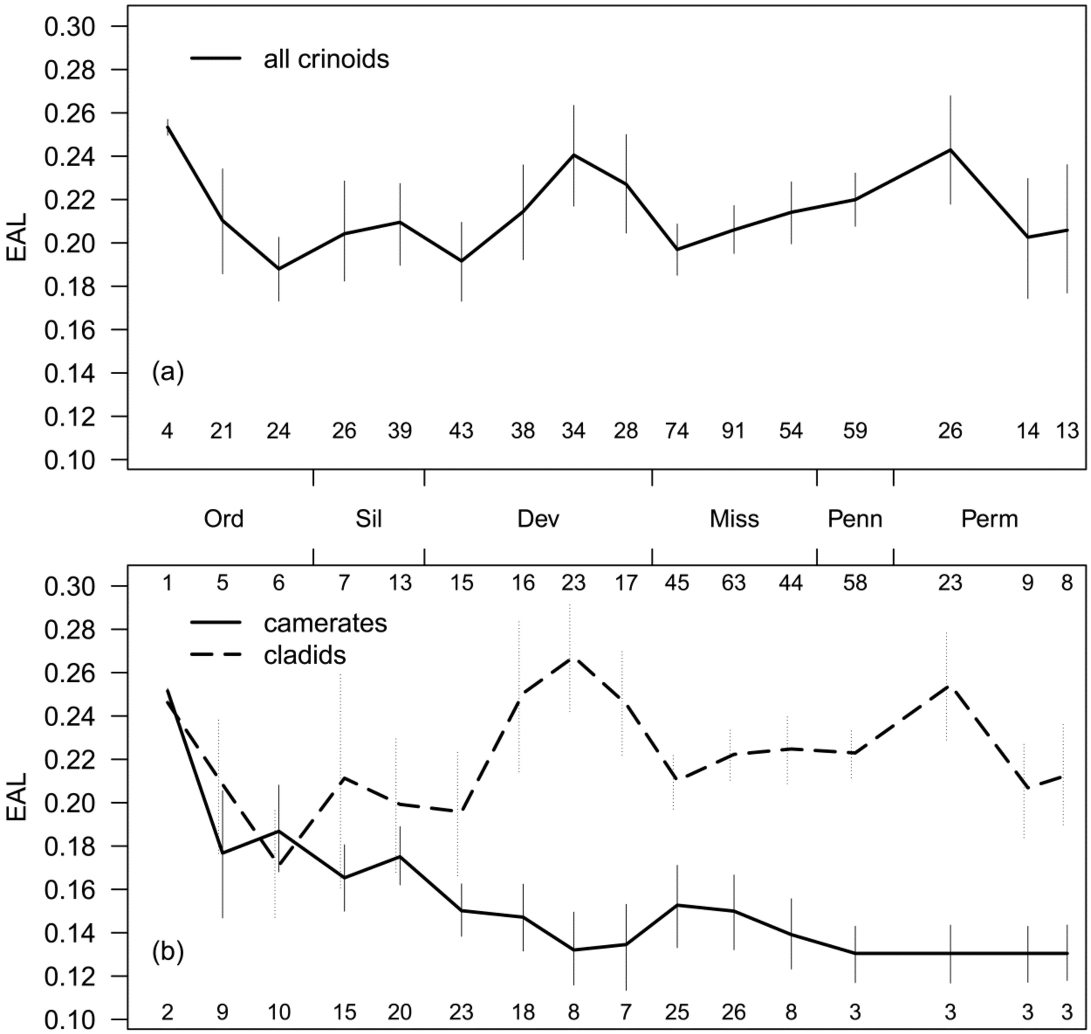


Figure III-4. Proportion of regenerating arms by period for all camerates and cladids. Data from Gahn and Baumiller (2004).

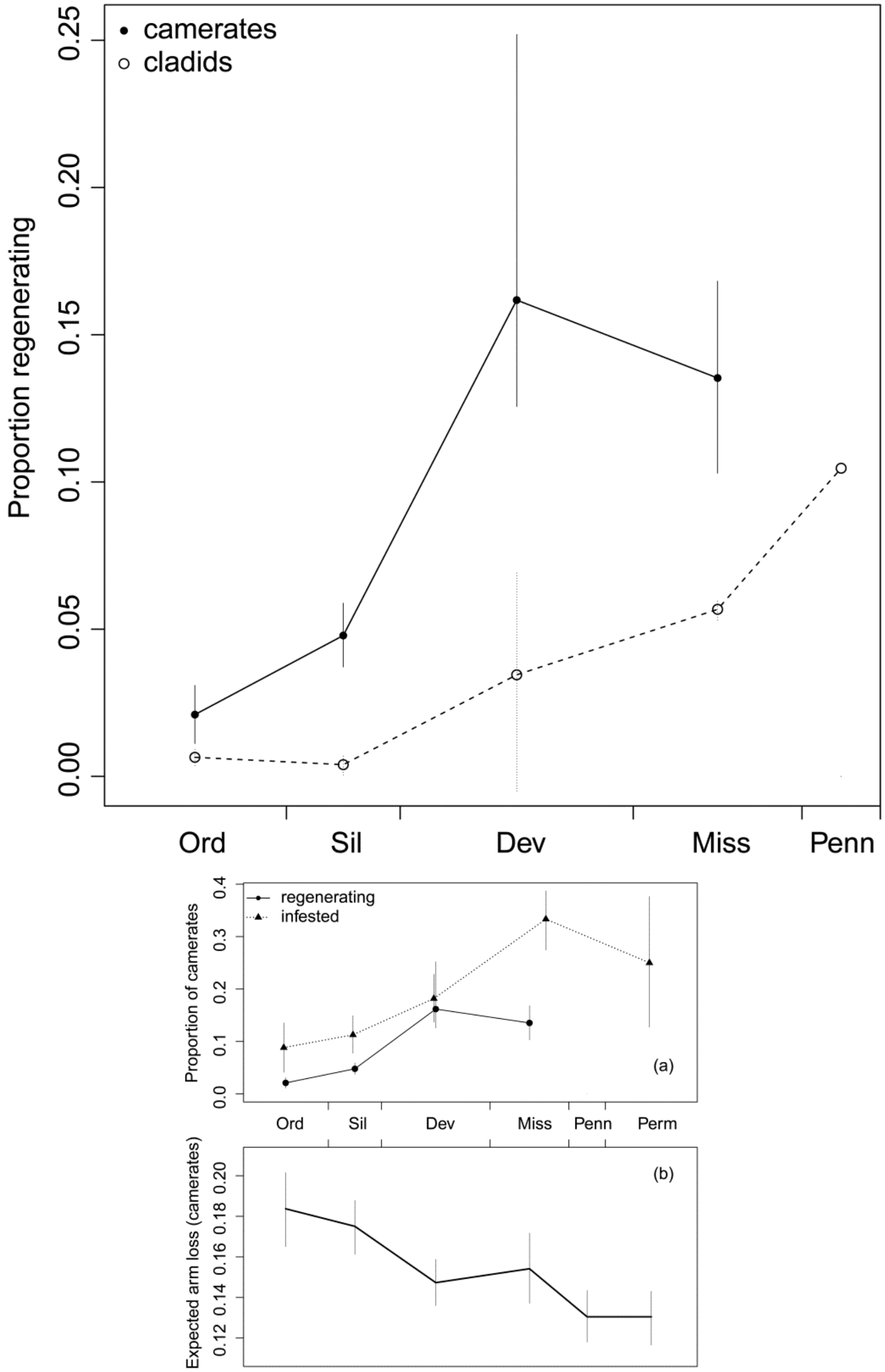
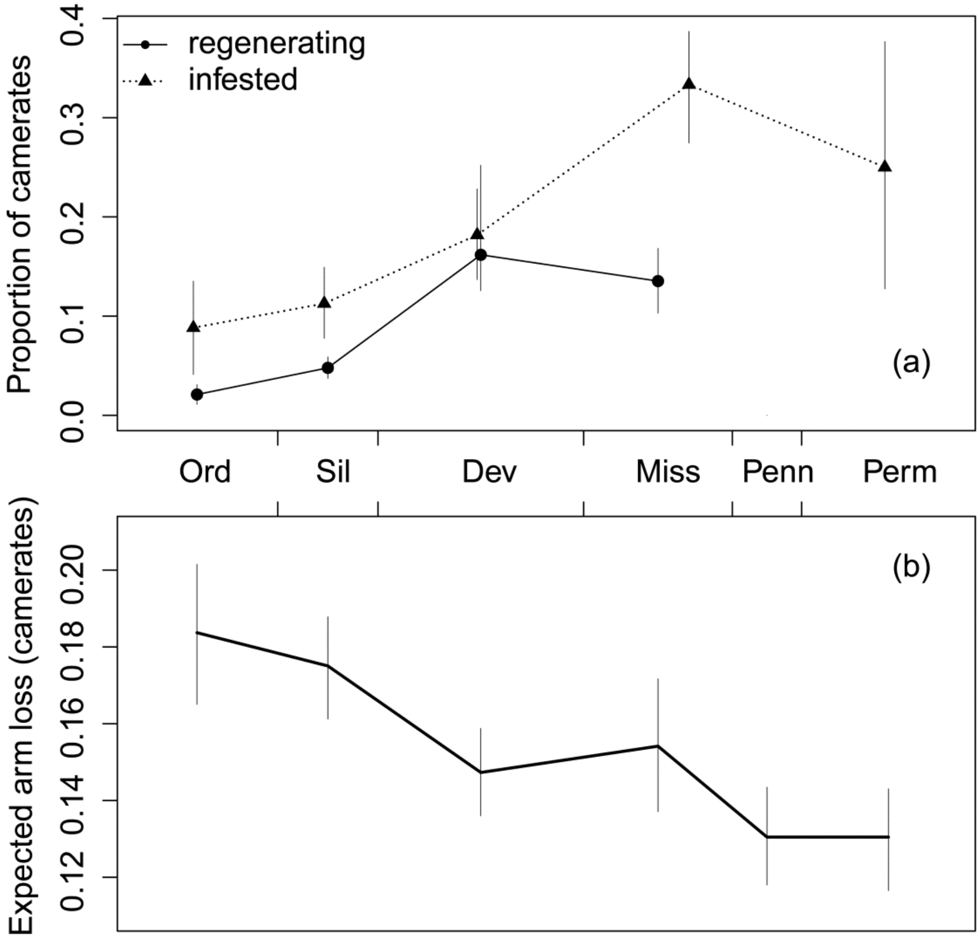


Figure III-5. Arm regeneration and platyceratid infestation frequencies in camerates (A) compared with camerate EAL values (B). Period time bins.



Tables

Table III-1. Tests for bias due to data source and preservation quality (Mann-Whitney *U*-test; H_0 = no difference/no correlation, U/U_{max}=0.5); significant results indicated by boldface. Measurements from photographs were tested against measurements taken directly on the specimens of which the photographs were taken. Brokenness was based on whether the longest such length was on a broken arm; difference between broken and unbroken specimens was borderline significant, but the effect was not large.

	N ratio	*p*-value	U/U_{max}
Treatise ~ collection photos	198:32	0.33	
Photographs ~ specimens	31:31	0.96	
Broken ~ unbroken	79:150	**0.06**	0.4232

Table III-2. *p*-values of Spearman rank-order tests for correlation of crinoid EALs with age and specimen size, calculated on the basis of maximum arm length from radial to tip (H_0 = no correlation). Significant results indicated by boldface; these results were not sensitive to the choice of correlation function. Correlation of EAL with age was significant only for camerates; when split according to the apparent change in trend in the Late Devonian, the correlation was even stronger and more significant for camerates during the first half of the Paleozoic, and not significant during the second half. Correlation of EAL with size was significant only for cladids.

	All	E Ord – L Dev	L Dev – L Perm
All crinoids ~ age	0.96	0.78	0.18
Camerates ~ age	**$<10^{-5}$ (ρ = 0.94)**	**$<10^{-15}$ (ρ = 0.93)**	0.11
Cladids ~ age	0.64	0.43	0.92
All crinoids ~ size	0.36		
Camerates ~ size	0.94		
Cladids ~ size	**$<10^{-3}$ (ρ = -0.30)**		

Table III-3. Frequency of regenerating arms and of infestation in camerates and cladids. Significant results indicated by boldface. Regenerating arms are significantly more common in camerates, and less common in cladids, than expectation. If regenerating arms are accepted as a proxy for injury by predators, then this indicates that predators preferred camerates over cladids as prey. Infesters show a significant preference for camerates over all non-camerates and over cladids in particular. Data from Baumiller and Gahn (2004).

	Camerate	Cladid	$p\ (\chi^2)$
Regenerating	160	31	**$<10^{-7}$**
Total	1381	652	
Infested (individuals)	17	5	**0.017**
Total (individuals)	44	35	
Infested (genera)	17	5	**$<10^{-3}$**
Total (genera)	44	53	

Table III-4. Frequency of regeneration in genera with infesting platyceratids versus those without. Significant results indicated by boldface. Genera known to be hosts are significantly more likely to be injured than those on which no parasites have been found. Data from Baumiller and Gahn (2004).

	Infested	Uninfested	$p\ (\chi^2)$
Regenerating (genera)	15	26	**0.0082**
Total (genera)	23	76	
Regenerating (individuals)	109	89	**$<10^{-7}$**
Total (individuals)	869	1488	

Chapter IV.
Spine breakage and regeneration in the Middle to Late Paleozoic

V. J. Syverson, Anna Reed, Forest Gahn, Tomasz K. Baumiller

Abstract

Sublethal injury that produces visible regeneration is frequent in both extinct and extant crinoids, and can be used to assess changes in predation intensity through time. Regeneration frequency in the arms of intact crinoids is often used as a proxy for the intensity of predation, but with appropriate adjustments the same technique can be used on disarticulated ossicles. Here we calculate regeneration frequency for two populations of disarticulated spines identified respectively as a Devonian camerate and a Pennsylvanian through Permian assemblage of indeterminate cladids. Both populations of spines exhibited per-part regeneration frequencies in the range of 5-15%, values similar to high Paleozoic and low to moderate modern crinoid arm regeneration frequencies. Separating the data by anatomical location of the spines gives a result consistent with a change in predator strategy between the Devonian and the Mississippian. Regeneration is more common in the Pennsylvanian than in the Permian, consistent with either a drop in predation or an increase in fatal predatory encounters.

Introduction

Echinoderms' prodigious powers of regeneration make it possible for predators to graze repeatedly on body parts without killing the organism, a mode of interaction referred to as "partial predation" (Vermeij 2002). Counting the frequency of damaged and regenerating body parts, under the assumption that most nonlethal damage is the result of partial predation (see Chapter I), therefore provides a proxy for the intensity of predation (Baumiller and Gahn 2013). In crinoids, this is usually done with arms, which are numerous, extend far from the body and are known to be damaged frequently during interactions with predators. However, crinoids can regenerate almost any body part, allowing the same estimate to be made for different kinds of predation resulting in different characteristic sets of injuries. In this study, a regeneration frequency is estimated for spine-bearing ossicles from the radials, aboral cup, tegmen, first primibrachs, and anal sac of two groups of Paleozoic crinoids.

Observed modes of predation on stalked crinoids include those of benthic predators, such as echinoids and presumably asteroids (Mladenov 1983; Baumiller et al. 2008); arm- or pinnule-grazing partial predation by nektonic predators, possibly targeting gonadal pinnules or infesting organisms (Fishelson 1974; Lane 1984; Meyer 1985); and direct attack on the visceral mass by swimmers (Meyer 1985; Schneider 1988; Lawrence and Vasquez 1996). All of these, at least in modern crinoids, usually result in nonfatal injury and regeneration. Mortality due to predation, though observed occasionally (Meyer 1985), is rare enough that it may be an occasional accident resulting from partial predation; furthermore, this circumstance does not seem unique to comatulids, since the combination of very low mortality with detectable frequencies of partial predation is also found in deep-sea cyrtocrinids, as discussed in Chapter II. In modern articulate crinoids, lethality requires disruption of the aboral nerve center (Ubaghs et al. 1978). Modern isocrinids have been observed to regrow nearly the entire body after the removal or autotomy of everything but the base of the calyx, including the entire visceral mass (Amemiya and Oji 1992). Paleozoic specimens belonging to extinct subclasses have been found regenerating after injuries of comparable severity, which indicates that Paleozoic crinoids shared the ability to survive and regenerate after losing most of the calyx, although in camerates this process appears to have produced growth anomalies in plate size and number (Gahn and Baumiller 2010).

Unfortunately, fatality, nonfatal loss of nearly the entire body, and postmortem breakage are generally indistinguishable in un-regenerated fossil material. We are therefore constrained to estimate the frequency of only those interactions that fulfill all of the following conditions:

a) Ossicles are broken during the attack.
b) The ossicles are not lost entirely in the attack.
c) The organism kept those ossicles for long enough afterwards that visible regeneration took place.

For brevity, we call this "regeneration frequency".

It is evident that the relationship between observed regeneration frequency and the actual frequency of predatory interactions is not straightforward. Despite its limitations, though, such a measure of partial predation can still be expected to reflect overall changes in predation (Vermeij 2002; Baumiller 2013). We therefore expect regeneration frequency to increase over intervals during which the intensity of predation is otherwise thought to increase. Here we examine samples of disarticulated crinoid ossicles representing the times of peak diversity (Figure I-2), spinosity (Figure V-1), and arm regeneration frequency (Figure III-4) for their subclasses, in order to assess whether the frequency of regeneration resulting from crushing predation might have been a source of selective pressure.

Data and Methods

We examined disarticulated crinoid spines from the Middle Devonian (n=176) and Middle Pennsylvanian through Lower Permian (n=1178). Spiny ossicles were sorted by anatomical location, by whether they were broken or not, and by whether the broken spine was regenerating. Anatomical locations are given specifically in Figure IV-1 and counts for all subsets are given in Table IV-1. Devonian specimens were from the Bell Shale in Alpena and Presque Isle counties in Michigan, USA, currently housed in the University of Michigan Museum of Paleontology (UMMP), and were identified as *?Gennaeocrinus goldringae*

(Camerata – Monobathrida) (Kesling 1965). Pennsylvanian and Permian specimens were collected by Moore and Jeffords (1967) from several locations in the southern Great Plains of North America, paleogeographically the shelf of the Pennsylvanian Midcontinent Sea (Algeo and Heckel 2008). Taxonomy at the genus level for the Pennsylvanian through Permian assemblages could not be ascertained reliably, but all specimens measured were of suborder Poteriocrinina (Inadunata – Cladida). The measurements taken were width and depth at base, length from base to point of regeneration if applicable, length from base to point of breakage if applicable, and total length.

We assumed that all examples of regenerating spines represent nonlethal interactions with predators. However, many recovered spines were broken without any sign of healing or regeneration at the broken surface, indicating either partial or total loss of the cup or anal sac or postmortem damage. Such loss or damage would artificially lower the observed regeneration frequency (R_{obs}), because the broken-off, unrecovered distal portions of those spines might have been regenerating from a previous injury before they were lost. Thus, including those spines in the analysis would produce a lower regeneration frequency than that which would have characterized the living population (true regeneration frequency, R_{true}). For example: If a sample experienced postmortem damage such that on average the recovered spines were 75% of their original length (completeness, $C_{avg}=0.75$), and R_{obs} in that sample is 0.1, then if we assume that the missing portions of the spines had a regeneration frequency similar to that of the recovered portions, then R_{true} can be estimated as $R_{obs}/C_{avg} = 0.1/0.75 = 0.13$. The true regeneration frequency was therefore estimated for each population of spines by the following procedure:

1) The ratio of length to the square root of (width × depth) at the base (i.e. the largest base diameter and that perpendicular to it) was calculated for all unbroken specimens of each anatomical type. This value was then used to estimate the maximum lengths (L_{max}) of all broken specimens from measurements of their base.

2) For each spine, completeness (C) was calculated as the ratio of its observed length L to L_{max}; all regenerating spines were treated as "complete" (C = 1.0).
3) For the entire sample, the average length of spines preserved was calculated as $C_{avg} = (\Sigma C) / n$, where n is the total number of spines with bases present in the sample.
4) The true regeneration frequency for the sample was estimated as the ratio $R_{obs}/C_{avg.}$

For comparison, regeneration frequencies were also computed using the empirical distributions of break length for regenerating and non-regenerating injuries. These alternative methods, which are documented in Appendix III, were more complicated and did not produce significantly different estimates.

Results

In the Pennsylvanian and Permian assemblages, 98% of spines were broken and 7.9% were regenerating. When these values are adjusted for postmortem breakage following the procedure described above, the estimated true regeneration frequencies are 9.4% for first primibrachial spines and 6.2% for anal sac spines, with the former more frequently broken in all intervals. Estimated true regeneration frequencies separated by time (Middle Pennsylvanian, Upper Pennsylvanian, and Lower Permian) are given in Table IV-1 and plotted in Figure IV-2. Differences in frequency between consecutive pairs of time intervals are given in Table IV-2; these were calculated using the simulation-based method described in Appendix C. For both types of spines, breakage frequencies were highest in the Upper Pennsylvanian and lowest in the Permian.

Among the Devonian specimens, unadjusted frequency of breakage was 59% and that of regeneration was 13%. Observed regeneration frequencies varied by anatomical type, as given in Table IV-1. For the reason discussed above, these regeneration frequencies are probably underestimates; in this case, however, the length and base measurements were not taken, so we could not compute a similar adjustment for postmortem breakage.

Discussion

Approximately 5-15% of spines are regenerating in all samples, consistent with other indications that crinoids were subject to substantial levels of nonlethal predation throughout the Middle Paleozoic. This value is similar to the highest known estimates of per-arm injury frequency in shallow-water crinoid populations from the Paleozoic, such as that of *Rhodocrinites kirbyi* from the Mississippian Le Grand formation (Baumiller and Gahn 2013), and to the lower end of estimates from living populations, such as *Florometra serratissima* between 79 m (18%) and 209 m (4%) (Baumiller 2013), and *Endoxocrinus* sp. from >500m depth (Oji 1996).

A substantial number of authors have produced data on frequencies of regeneration in modern and fossil taxa (Lawrence and Vasquez 1996; Baumiller and Gahn 2004), but most of these, especially for fossils, are per-individual probabilities of injury, which cannot be compared directly across taxa (Baumiller 2013). In this case we have neither a per-individual probability of injury nor a per-individual loss rate, because the samples consisted entirely of disarticulated ossicles. If we were to assume the number of each type of spine recovered from each individual in the population, such that we knew the number of individuals present, and also assume that injuries follow a binomial distribution among individuals, it would be possible to estimate the per-individual regeneration frequency. However, the first assumption may not hold true for anal sac spines, and the validity of the second is dependent on the details of the predatory interaction. We therefore restrict the comparisons here to those studies in which per-part injury frequencies have been collected.

Regeneration frequency is higher for first primibrach spines than for anal sac spines during all intervals in the poteriocrines, and higher for oral than for aboral spines in *?G. goldringae*. This is coincident with the appearance of angular crushed shell fragments in Mississippian shell beds and regurgitalites (Salamon et al. 2014) and an apparent relaxation of the selective pressure toward arm morphologies resilient to cropping (Chapter III), which is consistent with the hypothesis of a change in the primary target and mode of predation from (possibly commensal-associated) cropping of the arms and tegmen in the Devonian to attempts to crush and consume the calyx during the Pennsylvanian, as suggested by Sallan et al. (2011; 2013). It does not concord well with the hypothesis of Lane (1984) that the gonadal and visceral tissues were the preferred food of Paleozoic predators with the anal sac in cladids serving to place this high-value target further from the rest of the body. Such a pattern still might be seen if spines were an effective deterrent to anal-sac-cropping predators, though. In that case we predict that injured and regenerating intact anal sacs would be found more often in those cladid taxa where they are not protected by spines; no data have been collected to test this, although specimens with regenerating anal sacs exist (Gahn and Baumiller 2010).

For both types of spines in the poteriocrine data set, regeneration frequency in the Permian is significantly lower than in the Pennsylvanian. The proportional diversity of spiny cladid genera also falls from the Pennsylvanian to the Permian (Chapter V). It is possible that these fluctuations in regeneration frequency are particular to the shelf of the Midcontinent Sea and the coincidence with the global drop in proportional dominance of spiny cladid genera is accidental. We suggest, however, that the decrease in regeneration frequency from the Pennsylvanian to the Permian, combined with a decrease in frequency of spines among cladids, corresponds to a decrease in the intensity of predation on crinoids at this time. This decrease could be produced by two very different changes in the crinoid-predator relationship, depending upon the type of predatory interaction responsible for the regenerating injuries: either (1) overall interactions between crinoids and predators may have become less common, or (2) a change in predator behavior or in the dominant group of predators may have replaced nonlethal attacks with lethal attacks.

The most straightforward explanation is that predation on crinoids, or durophagous predation in general, became less common between the Pennsylvanian and the Permian; under such circumstances, we would certainly observe less frequent damage and regeneration. This is not the pattern predicted by the escalation hypothesis, which expects predation to increase throughout the Phanerozoic interrupted only by mass extinctions. It is unclear, though, why crinoids would become less favored as prey over this interval.

Any explanation based on decreasing crinoid abundance is misplaced: globally, the Late Paleozoic decrease in crinoid diversity (Figure I-2B) and disparity (Foote 1999) and the disappearance of encrinites (Greene et al. 2012) occur during the Late Mississippian, before the earliest of the collections explored in this study, and would therefore not be expected to have an influence, while the Pennsylvanian-Permian is an interval of peak cladid diversity (Figure I-2B). Other studies have indicated that the Camerata are preferred as prey over the Cladida in those intervals and localities where both are present (Gahn and Baumiller 2003) (Chapter III); however, no material identifiable to camerates is present in the collections studied here.

Alternatively, predator feeding strategy may determine the type of nonlethal injuries resulting from predation, regardless of the actual frequency of predation. If regeneration frequently results from failed attempts at more complete predation, then if a mode of attack more likely to result in regenerating injury was replaced by one more likely to result in nonregenerating injury, the frequency of regeneration would drop regardless of any change in the frequency of attack. In this case, though, there is no documented change in predatory behavior coincident with the decrease in nonlethal injuries.

Conclusions

The disarticulated specimens measured here constitute evidence for a persistent 5-15% frequency of proximal spine regeneration in crinoids of the dominant taxa before and after the Devonian-Mississippian transition. This is comparable to the highest frequencies of arm regeneration found in other Paleozoic crinoids and moderate-to-low frequencies in the Recent. However, specific comparisons to regeneration frequencies in other systems are difficult because of possible differences in the relationship between predation and regeneration, as well as the problem of normalizing per-part to per-individual regeneration frequencies. Our results are consistent with the scenario discussed in Chapter III, in which Devonian predators preferentially targeted camerate arms or arm-dwelling commensals and Carboniferous predators targeted the cups of cladids. Regeneration in poteriocrinine spines is less common in the Permian than in the Pennsylvanian, which may indicate either a drop in predation or a shift in predator ecological dominance, but further work will be required to determine whether the data here are representative of global changes in predator-prey relations.

Figures

Figure IV-1. Crown anatomy of *Gennaeocrinus goldringae* and a poteriocrine (the two crinoid taxa to which the spines in this study are referred), with presumed locations of the spines highlighted. A. *Gennaeocrinus goldringae*, with dorsal, radial, and oral spines labeled. From *Treatise on Invertebrate Paleontology* (Moore et al. 1978). B. Poteriocrinina (drawing is of a generalized pirasocrinid). First primibrach spines and anal sac spines labeled. Redrawn by the author after *Treatise on Invertebrate Paleontology* (Moore et al. 1978).

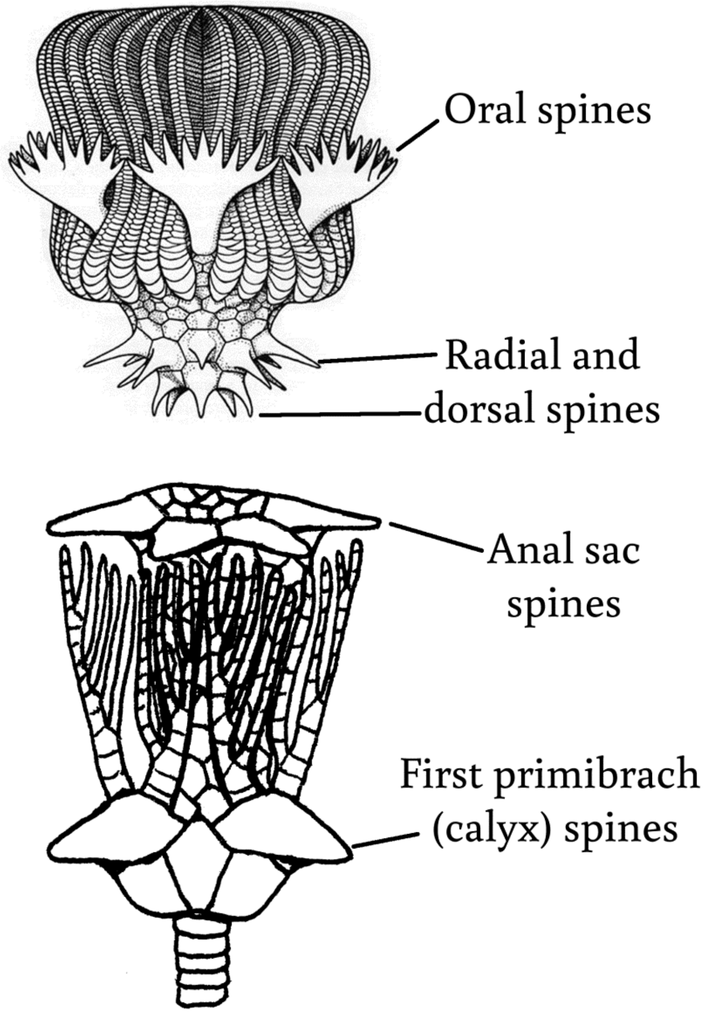
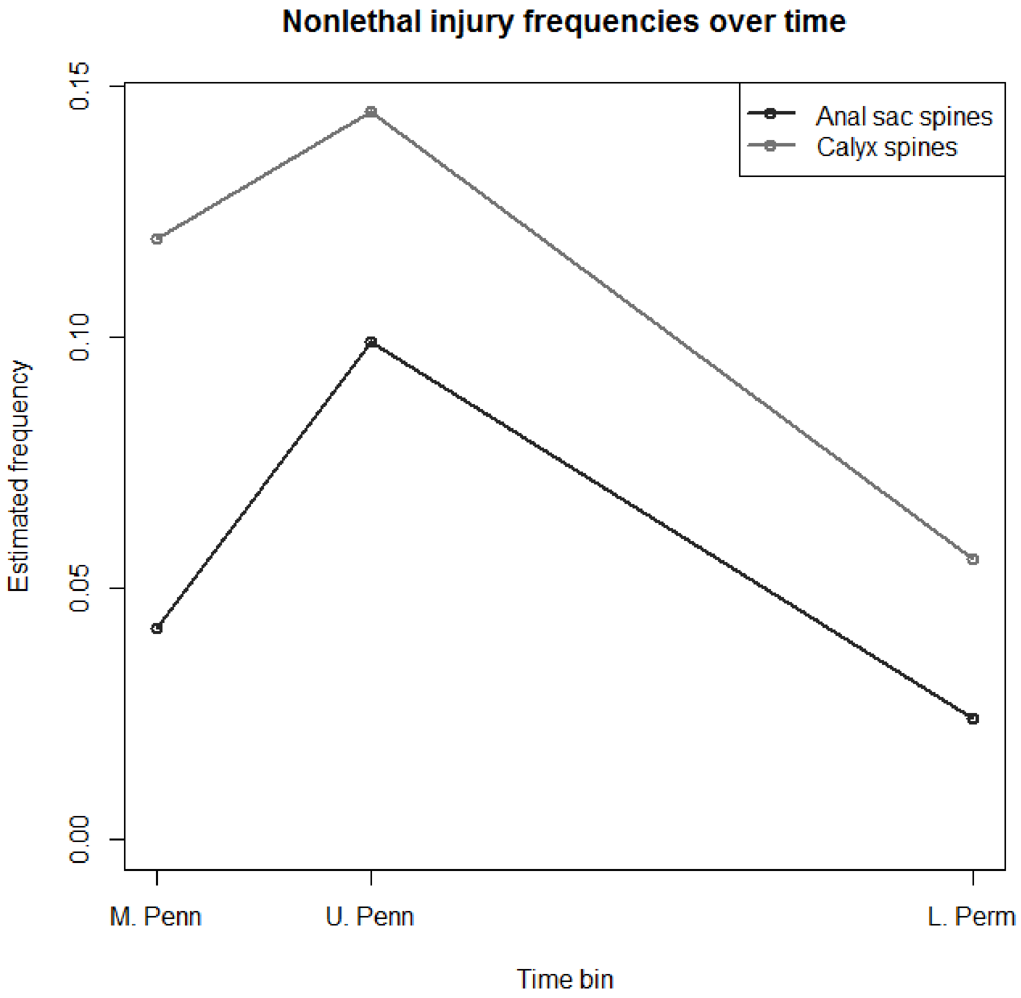


Figure IV-2. Estimates of true spine regeneration frequencies for specimens from Pennsylvanian and Permian poteriocrine assemblages, separated by time period. Values are given in Table IV-1.



Tables

Table IV-1. Regeneration frequencies for populations of disarticulated spines. The observed regeneration frequency and distribution of breakage locations were used to infer the true frequency of nonlethal damage in the living population. For details on the method of estimation, see text.

Taxon	Age	Anatomical type	n	Obs. breakage freq. (%)	Obs. regen. freq. (%)	Est. true regen. freq. (%)
?Gennaeocrinus goldringae (Camerata - Monobathrida)	M. Dev	All	176	59.1	12.5	
		Oral	60	53.3	20.0	
		Dorsal	69	43.5	11.6	
		Radial	47	89.4	4.3	
		Aboral cup (dorsal + radial)	116	62.1	8.6	
Poteriocrinina (Cladida)	All	All	1178	97.8	6.8	
		Anal sac	430	99.5	4.9	6.2
		1st primibrach	748	96.8	7.9	9.4
	M. Penn	Anal sac	54	98.1	3.7	4.2
		1st primibrach	460	96.3	10.0	12.0
	U. Penn	Anal sac	211	99.5	7.6	9.9
		1st primibrach	12	100	8.3	14.5
	L. Perm	Anal sac	157	100	1.9	2.4
		1st primibrach	232	96.3	4.7	5.6

Table IV-2. Magnitude and significance of differences in estimated injury frequencies between time bins for poteriocrine spine sample. Significances are estimated using the simulation method presented in Appendix C.

Anatomy	Time bin 1	Time bin 2	Difference (%)	Signif. (t-test)
Anal sac	M. Penn	U. Penn	+5.7	$p<10^{-3}$
Anal sac	U. Penn	L. Permian	-7.5	$p<10^{-14}$
Cup	M. Penn	U. Penn	+2.4	$p=0.5$
Cup	U. Penn	L. Permian	-8.4	$p<10^{-3}$

Chapter V.
Spinosity in Middle and Late Paleozoic crinoids and the timing of escalation during the Middle Paleozoic Marine Revolution

V. J. Syverson, Tomasz K. Baumiller

Abstract

The interval of increased shell-crushing predation and anti-predatory adaptation observed during the late Silurian through Carboniferous, referred to as the Middle Paleozoic Marine Revolution, has become more complex as observations have been added. Here we compile data on the occurrence of spines on different body parts in Paleozoic crinoid genera. We use these data to discuss the possible relationships between defensive adaptations in the different Paleozoic crinoid subclasses and the evolution of their enemies. Several phases in the development of these antagonistic biotic interactions are distinguishable over the course of the Paleozoic. A shift from Silurian to Devonian predators is apparent in the comparison of arm branching evolution (Chapter III) to spinosity. The differences in spinosity between Devonian and Mississippian crinoids support the hypothesis that tegmenal spines in crinoids result from "collateral damage" incurred in a three-way interaction between crinoids, parasites, and predators. The Pennsylvanian-through-Permian decrease in predation on cladids introduced in Chapter IV is supported, although its causes are still uncertain.

Introduction and Background

The Middle Paleozoic Marine Revolution (MPMR) was initially defined on the basis of an apparent coordinated increase in the diversity of durophagous predators and the proportion of taxa with anti-predatory adaptations in the Middle Paleozoic (Signor and Brett 1984). Among durophagous predators, the gnathostomes, phyllocarids, and eumalacostracans underwent radiations during the Devonian and Carboniferous; predatory ammonites and coleoids also appeared during this interval. Approximately coincident with these radiations, an assortment of predation-resistant morphologies became more frequent in other marine taxa, due to a combination of extinction and radiation: disjunct coiling vanished among molluscs while sculpture increased, crinoids acquired spines and thicker calycal walls, and spiny productid brachiopods diversified. Many of these defenses appeared as early as the Ordovician.

Later work has spread out these changes into a number of different phases, many of which have acquired names. The "Great Ordovician Biodiversification Event" (Webby 2004) corresponds to the rise of metazoan-dominated reefal environments and development of ecological tiering, with the primary predators being trilobites and orthoconic nautiloids (Servais et al. 2010), and established the Paleozoic ecological baseline from which these other increases proceeded; after this, mean body size continued to increase through the Silurian (Novack-Gottshall 2008). The "Devonian nekton revolution" (Klug et al. 2010) consists of an increase in occupation of the water column due to a diversification among active swimmers at the expense of benthic and demersal taxa and an increase in the sizes achieved by chordates (Payne et al. 2009), possibly associated with a rise in dissolved O_2 in the Early Devonian (Dahl 2010). After the depletion of the Middle Paleozoic crinoid fauna at the end of the Devonian, the "Age of Crinoids" was a brief interval during which some combination of favorable oceanographic conditions (Kammer and Ausich 2006) and decimation of predators during the late Devonian extinctions (Sallan and Coates 2011) produced a great abundance and diversity of new species in all crinoid groups, followed by an abrupt depletion of camerate diversity and a new cladid-dominated Late Paleozoic crinoid fauna as sea level fell.

By contrast, several analyses have found an overall ecological stasis over the Ordovician through Permian in a variety of indicators: the diversity of predators as a proportion of total diversity, niche occupation, incidence of parasitism, and frequency of drill holes (Bambach

2002; Baumiller and Gahn 2002; Bush et al. 2007; Huntley and Kowalewski 2007). However, this does not rule out the possibility of escalation among those predators and their prey being expressed as an arms race rather than as an overall ecological shift in the balance of power.

Spines as anti-predatory and anti-parasitic adaptations

Spines are a particularly obvious indication of predation; indeed, their proposed function as defensive armaments is one of the two main anti-predatory adaptations among crinoids associated with the MPMR. Although accurately determining the adaptive function of fossil morphologies can be difficult, in many cases it is possible to make a reasonable guess based on observed functions of similar structures in living organisms. Spines and other protrusions have multiple possible functions, but most proposals for their adaptive significance are loosely anti-predatory. Such growths have several possible defensive functions, such as increasing effective body size, distributing bite force, providing anchor for camouflage, and disrupting the settling of parasites and other epibionts. The functional morphology of spines depends heavily on their specific size and shape, and is beyond the scope of this study; all spines are treated as equivalent for the purposes of this study, regardless of specific proposed functions.

Other indicators of predation on crinoids have also been catalogued in previous studies. Direct evidence from regeneration of spines (Chapter IV) and of arms (Baumiller and Gahn 2004) reveals, among other things, a difference in the timing of increases in injury frequency in camerates and in cladids. Since stalked crinoids living in modern soft-bottom environments have few sources of injury other than predation, which is generally thought to be inflicted mainly by fishes, with some contribution from echinoids and possibly asteroids (Meyer 1985; Waters and Maples 1991; Gahn and Baumiller 2010), this is generally viewed as a good indicator for increasing predation. Chapter III discussed the optimization of arm branching patterns for increased resilience to partial arm loss, which show a similar divergence but whose changes occur much earlier. Decreasing numbers and increasing thickness of calyx plates, along with shrinking calyx size, may be linked to predation pressure, although the biomechanical underpinnings of these hypotheses have not yet been tested (Waters and Maples 1991; Simpson 2010). These changes occur not in the Devonian but in the late Mississippian with the ascendancy of the cladids. Anal sacs, which appeared in cladids around the same time, may also have served to decrease the damage done by partial predation (Lane 1984; Brett and Walker 2002).

Parasitism and predator targeting

Many genera of snails in the family Platyceratidae are commonly found on Paleozoic crinoids, usually located on the tegmenal surface, and often with deformations of the snail's growing margin implying long-term sessile residence. In some cases, they are associated with gastropod-type drill holes in the host's cup, indicating that they were capable of drilling (Baumiller 1990). The nature of the association has been proposed to be parasitic, kleptoparasitic, coprophagic, and/or gametophagic. However, the relationship appears to have been detrimental to the crinoid host, as infested crinoids were smaller than uninfested ones (Rollins and Brezinski 1988; Baumiller and Gahn 2002); this favours parasitism or kleptoparasitism.

Phylogenetic relationships imply that anal tubes in camerates may have evolved repeatedly as a deterrent to infestation later circumvented by drilling (Gahn and Baumiller 2001, 2006). As Brett and Walker (2002) observe, since many spiny crinoids (e.g. *Arthroacantha*) are among those most frequently infested by snails, spines appear not to have been a deterrent to infestation. Instead, the spines may have been a response to increased interest from predators due to the snail's presence. Some Middle Devonian and later platyceratids themselves had spines, which may have served a similar function, as in modern marine and terrestrial snails with a spiny or hairy periostracum, which may deter predators from swallowing them whole.

Here we compile data on the diversity of Paleozoic crinoid taxa with spines and compare the results to the above studies on other adaptations of crinoids to increasing predation and parasitism, in order to discuss possible connections between different changes in predator-prey interactions during the Middle Paleozoic.

Data and Methods

In the paper that first defined the MPMR, spinosity was shown to have increased in various lineages of crinoids during the middle Paleozoic. Subsequent research has produced a more detailed timeline of the various ecological changes taking place during the Paleozoic, and therefore it is potentially instructive to compare the timing of the events in these various data sets. However, the data presented in the original paper were recorded in physical media that are no longer accessible (Brett, 2013, pers. comm.). Therefore, in this paper, we have attempted to recreate and make available a data set on spinosity in crinoids comparable to that of Signor and Brett (1984), and to analyze it in the context of other recent discoveries about the MPMR.

Signor and Brett (1984) recorded the number of genera in the Macurda collections, Springer collections, and figures from Springer's monographs and Treatise on Invertebrate Paleontology for which any individual had sharp projections of any kind, and the locations of those spines (cup, arms or anal tube/sac). Nodules and tubercles were not included (Brett, 2013, pers. comm.). In this study, data were compiled on the presence and location of spines and nodes in crinoids during the Paleozoic, based on the plates and genus descriptions in the volume of the Treatise on Invertebrate Paleontology on Paleozoic crinoids and the plates from Springer's monographs on camerates and flexibles (Wachsmuth and Springer 1897; Springer 1920; Moore and Teichert 1978). For the *Treatise*, all descriptions including forms of the word "spine" and all apparently spiny specimens in figures were tabulated; in Springer's monographs, only the figures were used. This came to 100 genera total with any kind of spines. A further 5 genera were added based on spiny specimens in the UMMP invertebrate collection.

Anatomy was tabulated from descriptions and figures according to their apparent function; that is, spines associated with the anus were coded as "tegmen" except where an anal tube or sac elevated them above the oral surface, and spines on the first primibrach were coded as "cup" while those on any higher free brachial were coded as "arms". The presence of anal tubes was catalogued based on genus descriptions (Moore et al. 1978; Ausich et al. 2010), and the known occurrences of infesting snails on each genus were taken from previous work by Gahn and Baumiller (2006, 2010). Diversity curves were drawn from the temporal ranges and taxonomy of Paleozoic genera given by Webster (2003).

Results

The proportion of crinoids with spines, divided by subclass, is shown in Figure V-1. The first spiny genera occur in the Silurian; spines are most common during the Devonian through Pennsylvanian. The peak occurs during the Devonian through Mississippian for camerates, and Mississippian through Pennsylvanian for cladids. The standing diversities shown in Figure I-2 demonstrate that the rises and falls in proportion of spiny taxa do *not* coincide with the peak diversity for any of the subclasses; this is confirmed by correlations with $p>0.6$ for all time series.

Figure V-2 illustrates the anatomical location of spines over time in camerate (top) and cladid (bottom) genera. Cup spines were present almost exclusively in Devonian camerates, and spines on the anal structure in Carboniferous cladids. Nearly all spiny camerate genera throughout the Paleozoic had tegmenal spines. Higher likelihood of infestation by platyceratid snails is predicted by the presence of spines on the tegmen (0.28, $p=0.004$) and calyx (0.21, $p=0.04$), and by the absence of anal spines (-0.21, $p=0.004$). As previously remarked (Baumiller and Gahn 2004; Syverson and Baumiller 2014), infestation is much more common in camerates than in any other subclass ($p<10^{-11}$).

Discussion

Influence of Early Paleozoic predation

Spines first appear among crinoids in the Silurian, which is also the interval when arm branching in camerates is approaching more predation-resistant morphologies (Chapter III), and which precedes the usual definition of the MPMR. This is consistent with results from arm regeneration: although regenerating arms became more frequent in the Devonian, they are still observed in Ordovician and Silurian crinoids (Baumiller and Gahn 2004). This earlier rise of adaptations to predation in crinoids preceding the MPMR recalls the pattern observed in the Mesozoic Marine Revolution where benthic predators preceded nektonic, and therefore anti-predatory adaptations applying to benthic predation in crinoids, such as crawling and swimming, occurred before adaptations to nektonic predation in ammonoids and other swimming taxa (Baumiller et al. 2010). In both these cases, increases in predation on crinoids preceded the pulse of escalation more generally recognized as a “marine revolution”.

The decline of the Eurypterina, the predatory suborder of eurypterids, occurs at the same time as the diversification of gnathostomes, during the Early Devonian (Lamsdell and Braddy 2009). This shift in dominant predator is visible in cephalopods: coiled nautiloids diversify once in coordination with the emergence of eurypterids, and then reradiate and produce the ammonoids at the same time as the appearance of gnathostomes (Kröger 2005). Are the crinoid patterns related to the shift in dominant predators? If so, Ordovician and Silurian adaptations in camerate arm structure would imply that arm loss was a frequent consequence of non-fish predation, but camerate spinosity does not start increasing sharply until the gnathostome radiation in the Devonian. Calyx spines in camerates also became much less common after the late Devonian extinctions, when placoderms and sarcopterygians were largely replaced by sharks and actinopterygians. This allows us to suggest that the primary predators responsible for the appearance of spiny camerates are the placoderms and sarcopterygians of the Devonian vertebrate fauna.

Anal sac function

The anal sac is by far the most common location for spines in cladids, and peaks during their radiation in the late Mississippian and Pennsylvanian. In all intervals, all or nearly all cladid anal sacs were spiny (the ratio of cladids with anal sac spines to cladids with anal sacs did not deviate significantly from 1). This result is consistent with the hypothesis that the anal sac was a particular target of cladids' predators, far more than any other part of the body, and persistently through time.

Infestation and collateral damage

A much higher proportion of genera are spiny in the camerates than in any non-camerates. This is consistent with their higher rates of nonfatal injury, higher rates of infestation, and more predation-resistant arm shape (Chapter III), all of which indicate that camerates were under more evolutionary pressure from predators than members of other subclasses were. Greater food-gathering capability in camerates due to the presence of pinnules (Baumiller 2003) may have made them more desirable as both prey and hosts. What function their spines served in this three-way interaction, though, is a matter of interest.

Previous authors have noted an association between spiny crinoids and infesting snails (Brett et al. 2003, p. 131), but our data allow us to test this quantitatively and specify that the association is predicted primarily by spines located on the tegmen, and to a lesser extent on the calyx. The high correlation between tegmenal spines and infestation makes it seem unlikely that their purpose was to keep platyceratids from settling on the tegmen, but quite plausible that they served to repel those predators which were drawn by the presence of these infesting mollusks, as hypothesized by Brett (2002; 2003; 2004). Under this hypothesis, we expect tegmenal spines to follow the same frequency pattern as infestation in camerates. Gahn and Baumiller (2006) found that the number of infested camerate genera increases monotonically from four in the Ordovician up to a maximum of 24 in the Mississippian, and then drops to no more than three in the post-Mississippian. We therefore expect tegmenal spines in camerates to increase in frequency until the Mississippian and become far less common in the Pennsylvanian and later. This is indeed the pattern observed (Figure V-2). Tegmenal spines were no less common in camerates of the Early Mississippian radiation than in their Devonian predecessors; they do not decrease significantly in frequency until the Mississippian/Pennsylvanian. Furthermore, lower expected arm loss (Chapter III) is weakly but significantly associated with the presence of tegmenal spines ($R^2=0.1$, $p=0.007$) in camerates. The data reported here thus support the hypothesis that the function of tegmenal spines was to repel predators targeting platyceratids (and, potentially, other tegmen and arm infestors with lower preservation potential for which there are no data).

The function of spines on the aboral calyx in camerates is less apparent. Given their emergence in the Early Devonian alongside tegmenal spines, it seems likely they are also associated with the radiation of nektonic predators; they might easily be imagined as deterrents to fishes large enough to be capable of consuming the entire calyx. Since archaeocidaroid urchins originated around this time and may have been predators on crinoids at least as far back as the Carboniferous (Schneider 2001; Baumiller et al. 2008), it is also possible that some aboral calyx spines served to fend off attacks from below. However, since they become substantially less common after the end-Devonian extinctions, we infer that they are related to placoderm predation.

The widespread presence of spines among the crinoid genera that arose in the Early Mississippian radiation conflicts with the hypothesis of Sallan et al. (2011) that the diversification was the consequence of predatory release. It can be reconciled for the camerates by claiming that the most important predation suppressing their diversification was from placoderms attacking the aboral calyx, and that the predator-platyceratid-camerate interaction which persisted through the Mississippian was sufficient to produce selection but not to suppress speciation. In advanced cladids, though, the Mississippian diversification occurs despite no evidence for a decrease in predation; indeed, their increased spinosity appears to indicate the opposite. Furthermore, the precise ecological mechanisms behind this hypothesis are unclear: the frequency of predation that would be necessary to suppress speciation, and how long this would need to be relaxed in order to produce such a radiation as that of the Early Mississippian, are not well constrained. In order to validate the predatory-release hypothesis, a more concrete model of the effects of predation on prey diversification would need to be formulated.

Conclusion

A concordance of the different lines of evidence regarding predator-prey interactions in Paleozoic crinoids produces a picture somewhat more complex than the initial conception of the MPMR indicated. The emergence of spinosity in Paleozoic crinoids occurs in several phases which coincide with known developments in predator-prey interactions. These developments are summarized in Figure V-3.

During the Ordovician and Silurian, when the dominant predators were eurypterids and nautiloids, spinosity was very rare in all taxa and anatomical locations, although predation-resistant arm morphology was already on the rise. We infer that, although arm breakage was already frequent enough to advantage more efficient regeneration, the most common modes of injury did not often interact with the calyx.

During the Devonian, the replacement of eurypterids by placoderms as the primary durophagous predators and the increase in frequency of infestation by platyceratid snails resulted in a major increase in calyx and tegmen spines in crinoids. The former served as defenses against indeterminate placoderm attacks, but the latter are strongly associated with snail infestation, supporting the hypothesis of a three-way interaction in which collateral damage from predators targeting infestors drove the evolution of defenses in hosts.

In the Early to Middle Mississippian “Age of Crinoids”, the disappearance of the placoderms before the re-radiation of camerates meant that the new camerate genera were much less likely to have calycal spines. However, tegmen spines persisted until the end of the

Mississippian. We infer that collateral damage from predation on platyceratids also continued, meaning that either (a) the habit of preying on parasitic snails was taken up by the new vertebrate predators of the Mississippian or (b) the Devonian predators targeting the snails did not go extinct during the Late Devonian biodiversity crises. Differentiating these two possibilities would involve looking for associations between platyceratid-infested camerates and those predators which persisted from the Devonian into the Mississippian. The radiation of advanced cladids with large spiny anal sacs also occurred at this time, concurrent with the diversification of Mississippian predatory fishes.

From the Late Mississippian to the Permian, spinosity decreases among cladids. This is consistent with the spine regeneration frequencies from Pennsylvanian through Permian cladids reported in Chapter IV. However, as is discussed there, the cause of this drop in predation is uncertain; possibilities include a decrease in overall predation on crinoids or a change in the dominant predatory strategy that made spines a less effective defense against predation.

Figures

Figure V-1. Ratio of spiny genera to total genera within each time bin.

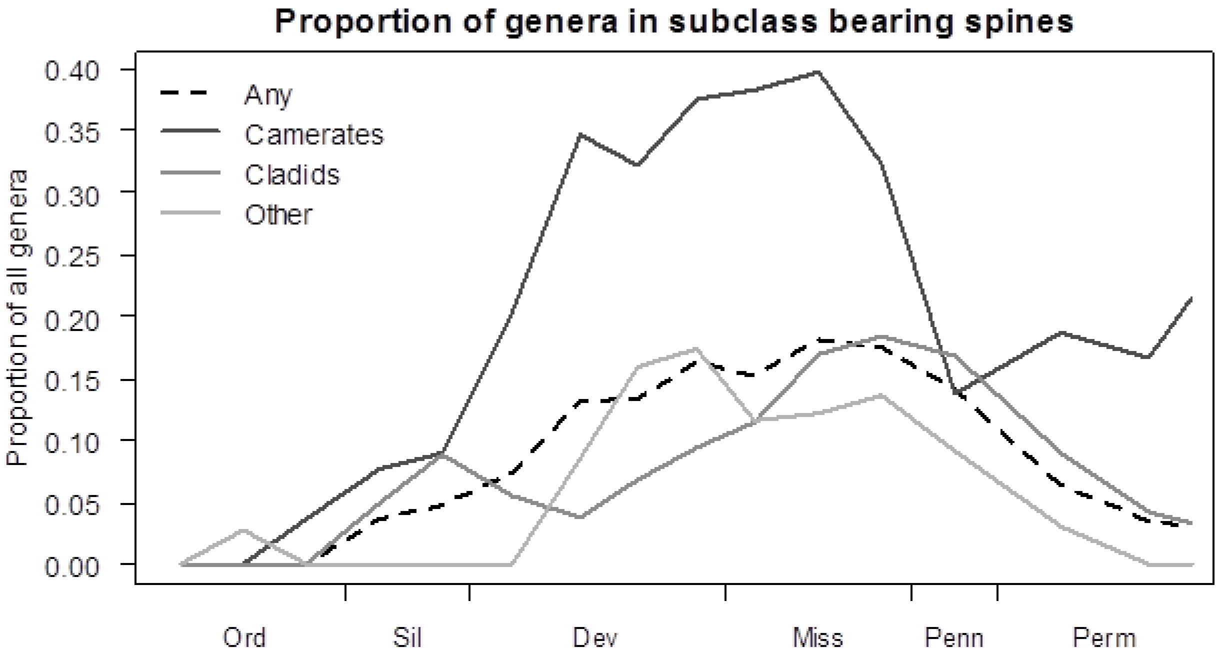


Figure V-2. Occurrence frequencies for spines on different body parts for camerate and cladid genera.

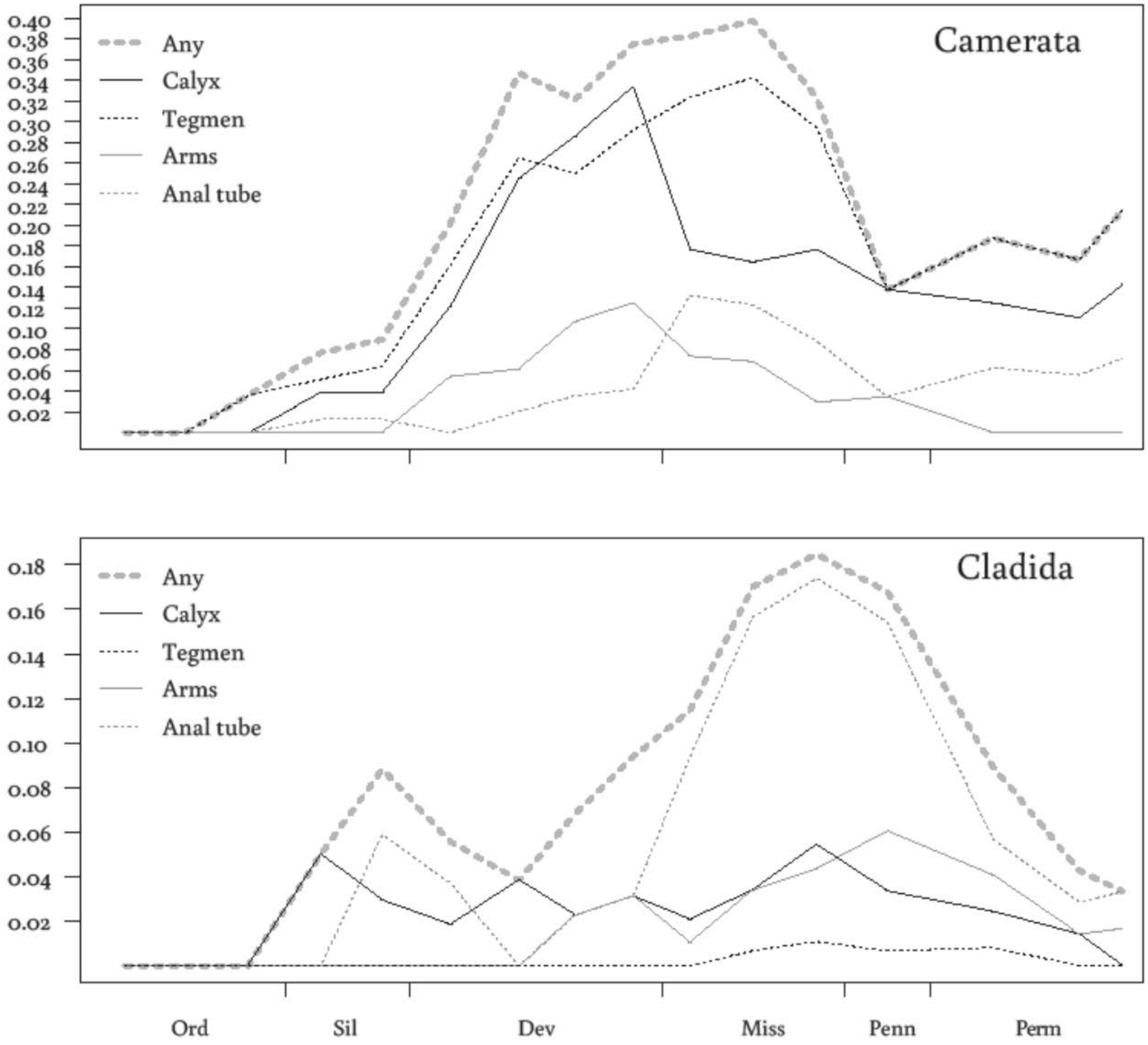
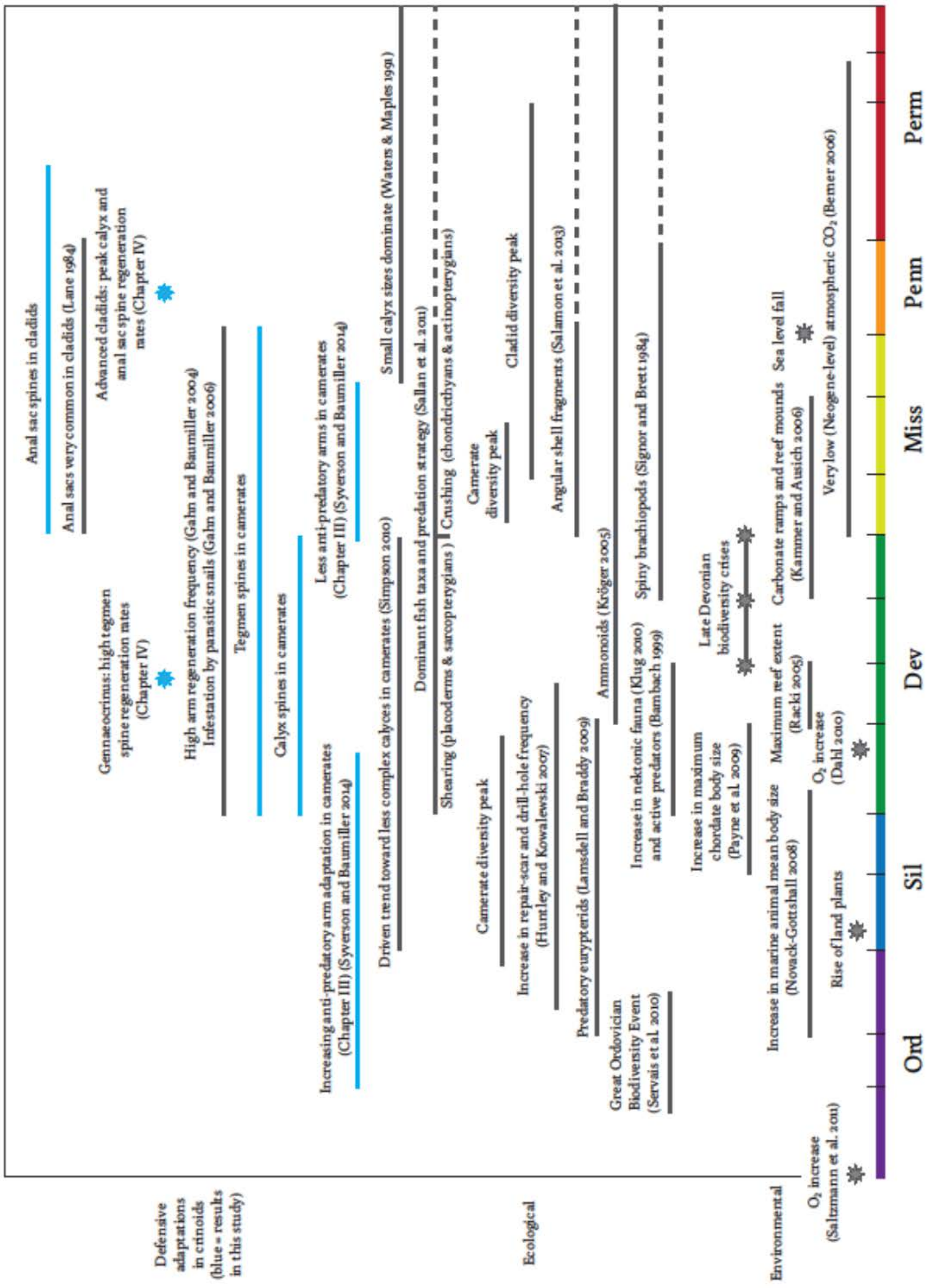


Figure V-3. Time or time range of occurrence for various events and patterns associated with the Middle Paleozoic Marine Revolution and the development of defensive adaptations in Paleozoic crinoids. Cyan lines indicate data original to this volume.



Chapter VI.
Conclusion

Antagonistic trophic interactions have undoubtedly influenced the course of evolution; the question of how and when is a matter of much paleontological interest. One influential idea is the hypothesis of escalation, which hinges on the idea that in the predator-prey relationship, predators have a disproportionate evolutionary impact on prey. It postulates that increasing predation has been the major selective pressure in the development of Phanerozoic life, driving the evolution of prey species and thus urging all elements of the biosphere continually toward higher energetic requirements (Vermeij 1987, Dietl 2003). The fossil record of crinoids, as a relatively constant and consistently non-predatory element of marine faunas over the Phanerozoic, provides a good study system for this phenomenon. In this study, we have investigated crinoid injury frequency and defensive adaptations during different intervals in order to test previous authors' hypotheses about crinoids' interactions with their predators and to illuminate the timing of escalation in this system.

A trend toward predator-resistant arm adaptations (decreasing mean EAL) is apparent as early as the Middle Ordovician. During the Ordovician this trend applied to all crinoids; however, during the Silurian it only occurred in camerates, which were at their first episode of peak diversity. Thus, although the Ordovician trend may have been driven by any abiotic or biotic cause of breakage, arm loss during the Silurian was probably resulting from camerate-specific interactions with predators. Silurian predators included eurypterids, nautiloids, and trilobites (Brett and Walker 2002), but not gnathostomes, cidaroids, or ammonoids. We therefore infer that one or more of these Silurian non-fish predators were preying on the arms of camerates.

Given the known association between camerates and platyceratids, it is possible that Silurian predators were targeting some kind of parasites; indeed, Vermeij (2002) suggests that parasitism may be an older form of consumption than predation. Crinoid-parasitizing platyceratids existed in this time period (Gahn and Baumiller 2002), and myzostomid worms may already have been parasitizing Ordovician crinoids (Warn 1976). However, the tegmenal spines associated with collateral damage from predators did not appear until the Devonian. More camerate taxa were infested by platyceratids during the Devonian, more had spiny tegmens, regeneration of arms and tegmen spines was more common, and EAL continued to drop; furthermore, these four indicators of preferred prey or host status all tend to coincide in particular camerate genera. The fact that all four appear at the beginning of the Devonian, when the radiation of jawed fishes took place, argues in favor of fish as the major predatory agents involved in producing this indirect effect.

We also infer that placoderms are the most likely predator associated with the presence of calycal spines, for similar reasons of timing. Taking all this into account, we can address the hypothesis of predatory release as a cause of the Mississippian crinoid radiation, as put forth by Sallan et al. (2011). According to this hypothesis, the diversity of Devonian camerates was kept low by the presence of a large diversity of predatory fishes, followed by release and radiation after those predators went extinct and before the re-radiation of their successors. Although the exact mechanism of the interaction between predator diversity and prey diversity remains to be explained, under that scenario, we would expect the camerate genera surviving through the Late Devonian diversity depletions to be increasingly well-defended, and the new post-predator-extinction genera to bear fewer anti-predatory adaptations. This pattern is visible in the camerate calyx spine time series. Tegmen spines in camerates, however, do not obey this prediction at all. We therefore conclude that the parasite-mediated interaction was either independent of specific predators or dependent on a predator taxon that was not disrupted by the Late Devonian extinctions. This interaction appears to have been closely tied to the camerates that were their preferred hosts, as it drops off after the late Mississippian.

We find strong support for previous reports of higher frequencies of predation and parasitism in camerates than in cladids during all periods when camerates were diverse. A decrease in predation between the Pennsylvanian and Permian is evidenced independently by spine regeneration frequencies and the occurrence of anal sac spines. As there is no obvious explanation for this pattern, a more detailed investigation would be necessary, first to validate its existence across a wider geographic range and then to consider potential causes.

The general tendency observed by many authors toward continually increasing levels of predation in marine ecosystems, and the attendant relegation of less active antique taxa to marginal environments, is visible in the records of crinoid regeneration frequencies as presented here. *Holopus* and its co-occurring confamilial *Cyathidium* are relics of a highly successful Middle Mesozoic order, of which the Jurassic members *Eugeniacrinites* and *Pilocrinus* appear to have had a frequency of nonlethal injury on the same order as that of *Holopus* in this study, with around 10% of individuals injured. This frequency is also comparable to that of some Paleozoic populations. However, the Paleozoic and Jurassic populations in question lived in a high-diversity, high-energy shallow sea environment, while *Holopus* today occupies a bathyal environment with a nutrient flow so slow that its growth rate is no more than a millimeter per year and it is injured by a predator on average once every 1.5 years. It is possible that Mesozoic bathyal cyrtocrinids existed and had similarly slow rates of growth, but no modern cyrtocrinids live in shallow water. For comparison, in modern shallow-water comatulid populations it is not unusual for 80-100% of individuals to be injured, and regrowth rates are two orders of magnitude higher than in *Holopus*.

Increasing predatory pressure has been one of the factors directing the evolution of marine life, especially the suspension feeders that constitute the majority of marine species (Bush et al. 2007). This dissertation investigated the nature and timing of escalation in crinoids, using regeneration as a proxy for predatory interactions and a variety of proposed anti-predatory adaptations, and more detail was provided on the stages of development in crinoid-predator interactions. Further work should focus on refining the interpretation of per-part versus per-individual regeneration frequencies, exploring the possible decrease in predation on crinoids in the Late Paleozoic, revising and improving platyceratid taxonomy in order to investigate the evolution of taxon specificity in host-parasite interactions, and obtaining data on specific regional- and community-level associations between crinoid and predator taxa.

APPENDICES

Appendix A: EAL data, origination and extinction dates

The following table gives the genus names and temporal ranges of all genera used in calculations for Chapter III, according to Webster (2003), and the EAL values and crown sizes, which were calculated as described in the text of the chapter based on measurements taken from images and specimens.

Genus	Subclass	origin (ma)	extinction (ma)	EAL	size
Abatocrinus	Camerata	359.2	340	0.13	22.0
Abrotocrinus	Cladida	348	318.1	0.16	69.0
Acacocrinus	Camerata	443.7	385.3	0.25	31.3
Acrocrinus	Camerata	333	318.1	0.20	48.0
Actinocrinites	Camerata	397.5	251	0.10	74.0
Acylocrinus	Cladida	348	340	0.28	21.3
Aethocrinus	Aethocrinea	488.3	471.8	0.26	52.0
Agaricocrinus	Camerata	359.2	340	0.25	36.4
Agassizocrinus	Cladida	333	318.1	0.27	54.3
Aglaocrinus	Cladida	318.1	299	0.15	61.4
Agnostocrinus	Cladida	299	265.8	0.16	66.0
Alcimocrinus	Cladida	333	308	0.08	76.0
Alisocrinus	Camerata	451	421.3	0.14	66.0
Allosocrinus	Cladida	308	280	0.50	53.6
Ambicocrinus	Camerata	422.9	397.5	0.13	26.0
Ampelocrinus	Cladida	333	311.7	0.17	77.4
Ampheristocrinus	Cladida	438	421.3	0.13	30.0
Anamesocrinus	Disparida	397.5	359.2	0.10	11.7
Anartiocrinus	Cladida	333	318.1	0.28	25.3
Anchicrinus	Cladida	318.1	306.5	0.14	54.5
Anomalocrinus	Disparida	471.8	443.7	0.11	73.8
Anthemocrinus	Camerata	428.2	422.9	0.16	18.5
Aorocrinus	Camerata	416	333	0.13	22.0
Aphelecrinus	Cladida	359.2	318.1	0.20	25.3
Apographiocrinus	Cladida	318.1	299	0.29	24.2
Arachnocrinus	Cladida	416	397.5	0.06	116.0
Archaeocrinus	Camerata	471.8	460.9	0.23	52.0
Arthroacantha	Camerata	416	359.2	0.10	84.3
Aryballocrinus	Camerata	359.2	340	0.20	71.0
Ascetocrinus	Cladida	348	340	0.16	57.0

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Aulocrinus	Cladida	348	333	0.27	68.0
Bactrocrinites	Cladida	443.7	385.3	0.18	26.4
Barycrinus	Cladida	348	333	0.28	52.9
Bathericrinus	Cladida	428.2	422.9	0.28	45.0
Batocrinus	Camerata	359.2	318.1	0.06	36.0
Belanskicrinus	Cladida	385.3	374.5	0.30	32.8
Belemnocrinus	Cladida	359.2	340	0.29	50.0
Blothrocrinus	Cladida	374.5	326.4	0.08	214.0
Bogotacrinus	Camerata	407	391.8	0.08	47.7
Bohemicocrinus	Camerata	422.9	416	0.19	33.0
Brabeocrinus	Cladida	311.7	280	0.18	36.0
Briarocrinus	Camerata	428.2	422.9	0.27	45.3
Bridgerocrinus	Cladida	385.3	345.3	0.32	20.0
Bronaughocrinus	Cladida	333	318.1	0.28	37.6
Cactocrinus	Camerata	359.2	340	0.14	70.0
Cadiscocrinus	Camerata	391.8	385.3	0.13	9.7
Carabocrinus	Cladida	471.8	422.9	0.16	68.9
Carcinocrinus	Cladida	333	318.1	0.23	90.0
Carpocrinus	Camerata	443.7	397.5	0.17	24.7
Catactocrinus	Cladida	385.3	374.5	0.50	27.5
Catillocrinus	Disparida	348	308	0.05	24.0
Cercidocrinus	Cladida	359.2	340	0.10	70.0
Cicerocrinus	Disparida	422.9	418.7	0.23	27.0
Clarkeocrinus	Camerata	397.5	385.3	0.08	58.0
Clathrocrinus	Cladida	311.7	305	0.28	50.4
Cleiocrinus	Camerata	471.8	460.9	0.03	1.0
Clematocrinus	Camerata	443.7	397.5	0.14	14.0
Clonocrinus	Camerata	438	397.5	0.15	55.0
Coeliocrinus	Cladida	348	340	0.17	25.3
Contocrinus	Cladida	308	275.6	0.29	28.2
Corematocrinus	Cladida	388	370	0.30	40.7
Corocrinus	Camerata	416	359.2	0.25	22.8
Corythocrinus	Cladida	348	340	0.17	65.0
Cosmetocrinus	Cladida	348	318.1	0.17	81.4
Cradeocrinus	Cladida	416	348	0.29	28.7
Cribanocrinus	Camerata	359.2	333	0.11	33.3
Cromyocrinus	Cladida	348	306.5	0.50	64.0
Culmicrinus	Cladida	374.5	318.1	0.22	67.0
Cupressocrinites	Cladida	443.7	374.5	0.50	40.0
Cupulocrinus	Cladida	460.9	411.2	0.15	30.0

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Cusacrinus	Camerata	359.2	340	0.08	42.0
Cyathocrinites	Cladida	428.2	251	0.14	16.0
Cydrocrinus	Cladida	348	340	0.10	86.0
Cymbiocrinus	Cladida	340	311.7	0.30	31.5
Cytidocrinus	Camerata	348	340	0.04	82.6
Dasciocrinus	Cladida	333	318.1	0.27	29.7
Decadocrinus	Cladida	391.8	305	0.30	50.0
Decorocrinus	Cladida	391.8	385.3	0.50	79.0
Dendrocrinus	Cladida	488.3	416	0.25	43.0
Desmidocrinus	Camerata	438	418.7	0.07	33.3
Diabolocrinus	Camerata	460.9	449	0.24	88.0
Diamenocrinus	Camerata	397.5	385.3	0.09	21.0
Dicromyocrinus	Cladida	318.1	299	0.27	84.0
Dinotocrinus	Cladida	359.2	318.1	0.20	27.3
Diphuicrinus	Cladida	318.1	299	0.29	50.8
Dizygocrinus	Camerata	348	340	0.06	45.0
Dolatocrinus	Camerata	407	385.3	0.25	76.0
Dorycrinus	Camerata	348	333	0.10	46.0
Dystactocrinus	Disparida	453	447.5	0.08	38.7
Ectenocrinus	Disparida	451	443.7	0.28	50.0
Eirmocrinus	Cladida	308	306.5	0.12	111.3
Enallocrinus	Cladida	428.2	422.9	0.04	111.4
Eratocrinus	Cladida	359.2	333	0.13	53.0
Erisocrinus	Cladida	348	251	0.27	80.0
Eucladocrinus	Camerata	348	340	0.32	100.0
Eudimerocrinus	Camerata	438	421.3	0.11	40.0
Eustenocrinus	Disparida	460.9	449	0.25	75.0
Eutrochocrinus	Camerata	348	340	0.06	22.0
Exocrinus	Cladida	308	280	0.24	15.0
Exoriocrinus	Cladida	308	299	0.24	107.1
Fifeocrinus	Cladida	345.3	326.4	0.13	76.0
Follicrinus	Cladida	416	359.2	0.17	98.0
Gaurocrinus	Camerata	460.9	443.7	0.17	20.0
Gennaeocrinus	Camerata	416	359.2	0.09	33.3
Gissocrinus	Cladida	428.2	391.8	0.17	27.3
Glyptocrinus	Camerata	471.8	421.3	0.25	123.5
Goniocrinus	Cladida	359.2	340	0.29	23.5
Gothocrinus	Cladida	428.2	422.9	0.29	32.0
Grenprisia	Cladida	471.8	460.9	0.28	37.2
Haeretocrinus	Cladida	308	299	0.18	66.7

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Hallocrinus	Cladida	407	374.5	0.08	86.7
Hapalocrinus	Camerata	422.9	397.5	0.26	101.4
Haplocrinites	Disparida	443.7	345.3	0.50	1.0
Heterocrinus	Disparida	460.9	443.7	0.22	18.0
Histocrinus	Cladida	359.2	340	0.28	58.6
Holcocrinus	Cladida	374.5	345.3	0.27	43.0
Hybocrinus	Disparida	471.8	460.9	0.50	64.0
Hydreionocrinus	Cladida	359.2	315	0.14	85.7
Hydriocrinus	Cladida	311.7	299	0.24	37.6
Hylodecrinus	Cladida	348	333	0.16	108.6
Hypselocrinus	Cladida	374.5	308	0.27	112.8
Ibexocrinus	Disparida	471.8	464	0.18	11.2
Imitatocrinus	Cladida	416	397.5	0.26	47.0
Iocrinus	Disparida	471.8	443.7	0.11	61.0
Isotomocrinus	Disparida	471.8	460.9	0.18	29.8
Jimbacrinus	Cladida	294.6	275.6	0.50	200.0
Lanecrinus	Cladida	348	299	0.30	11.0
Lasiocrinus	Cladida	416	348	0.16	25.0
Lebetocrinus	Cladida	348	333	0.10	106.0
Lecobasicrinus	Cladida	308	306.5	0.26	59.2
Lecythocrinus	Cladida	397.5	391.8	0.10	88.0
Lenneocrinus	Camerata	416	374.5	0.11	19.7
Linobrachiocrinus	Cladida	385.3	359.2	0.50	73.0
Linocrinus	Cladida	359.2	318.1	0.17	20.8
Lobalocrinus	Cladida	305	299	0.25	53.8
Logocrinus	Cladida	391.8	374.5	0.32	27.9
Lophocrinus	Cladida	345.3	326.4	0.50	74.3
Lyriocrinus	Camerata	438	421.3	0.25	42.0
Macarocrinus	Camerata	411.2	397.5	0.17	56.0
Macrocrinus	Camerata	359.2	333	0.17	35.4
Mantikosocrinus	Cladida	333	326.4	0.27	34.0
Marathonocrinus	Cladida	311.7	308	0.14	31.0
Marsupiocrinus	Camerata	443.7	411.2	0.13	32.0
Mastigocrinus	Cladida	428.2	418.7	0.18	111.4
Metacromyocrinus	Cladida	311.7	306.5	0.29	29.0
Microcaracrinus	Cladida	311.7	306.5	0.22	11.8
Mooreocrinus	Cladida	318.1	308	0.27	73.0
Moscovicrinus	Cladida	311.7	251	0.18	54.0
Myelodactylus	Disparida	443.7	397.5	0.09	53.3
Neoprotencrinus	Cladida	311.7	305	0.28	67.5

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Notiocrinus	Cladida	299	251	0.20	40.0
Nunnacrinus	Camerata	359.2	340	0.25	41.0
Nyctocrinus	Camerata	438	421.3	0.15	32.7
Ohiocrinus	Disparida	471.8	443.7	0.31	34.0
Oklahomacrinus	Cladida	311.7	299	0.28	34.3
Onychocrinus	Flexibilia	348	318.1	0.32	174.9
Ophiocrinus	Camerata	416	397.5	0.14	26.7
Opsiocrinus	Camerata	391.8	385.3	0.27	9.3
Oxynocrinus	Cladida	318.1	311.7	0.16	50.3
Pachylocrinus	Cladida	374.5	306.5	0.12	48.0
Paianocrinus	Cladida	333	318.1	0.22	28.3
Parabursacrinus	Cladida	299	251	0.15	47.0
Paracatillocrinus	Disparida	299	251	0.08	22.0
Paracromyocrinus	Cladida	333	305	0.28	94.3
Paradichocrinus	Camerata	348	340	0.12	94.0
Parastachyocrinus	Cladida	299	251	0.31	30.0
Parazeacrinites	Cladida	359.2	326.4	0.12	44.4
Parisangulocrinus	Cladida	416	397.5	0.13	63.0
Parspaniocrinus	Cladida	299	280	0.50	15.4
Parulocrinus	Cladida	308	280	0.23	29.3
Pegocrinus	Cladida	311.7	306.5	0.27	86.0
Pelecocrinus	Cladida	359.2	340	0.23	114.3
Pellecrinus	Cladida	348	340	0.28	59.0
Pentaramicrinus	Cladida	333	318.1	0.50	48.0
Periechocrinus	Camerata	438	385.3	0.08	160.0
Periglyptocrinus	Camerata	471.8	460.9	0.13	41.0
Phacelocrinus	Cladida	340	311.7	0.28	68.0
Phanocrinus	Cladida	333	280	0.27	55.0
Physetocrinus	Camerata	359.2	340	0.06	72.0
Pirasocrinus	Cladida	308	306.5	0.09	73.0
Pisocrinus	Disparida	443.7	385.3	0.50	34.0
Platycrinites	Camerata	416	251	0.15	38.9
Pleurocrinus	Camerata	348	251	0.14	37.8
Plummericrinus	Cladida	333	280	0.19	92.0
Porocrinus	Cladida	471.8	443.7	0.25	20.5
Poteriocrinites	Cladida	397.5	299	0.17	77.1
Praecupulocrinus	Cladida	471.8	443.7	0.10	50.9
Proexenocrinus	Camerata	478.6	471.8	0.25	33.3
Propoteriocrinus	Cladida	407	397.5	0.15	92.9
Protacrocrinus	Camerata	359.2	348	0.26	23.1

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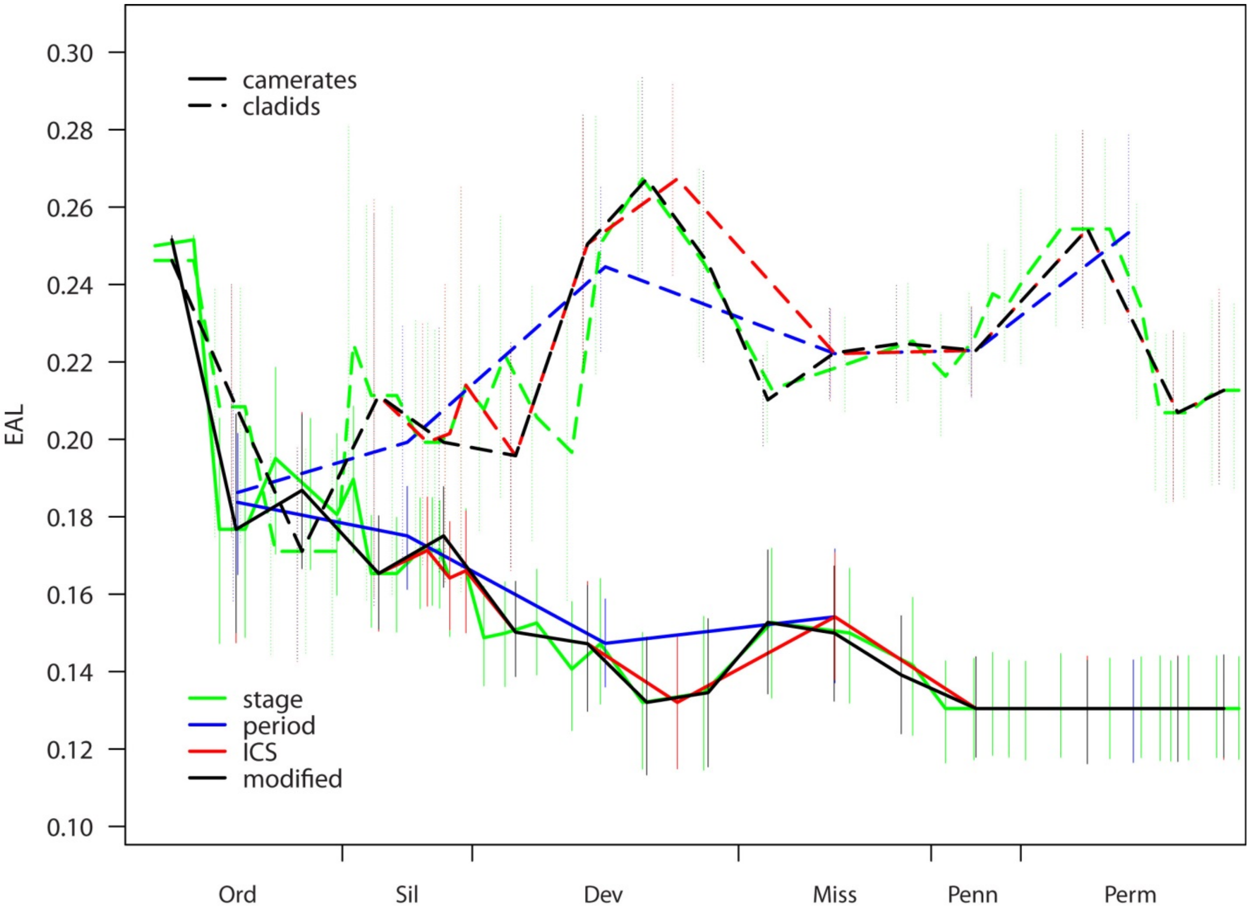
Protaxocrinus	Flexibilia	449	411.2	0.26	14.1
Protencrinus	Cladida	311.7	275.6	0.28	61.3
Pterotocrinus	Camerata	333	318.1	0.14	25.0
Ptychocrinus	Camerata	460.9	422.9	0.19	12.7
Pycnocrinus	Camerata	471.8	443.7	0.27	45.0
Quantoxocrinus	Cladida	391.8	359.2	0.38	28.6
Ramulocrinus	Cladida	359.2	318.1	0.29	27.3
Reteocrinus	Camerata	471.8	443.7	0.06	37.8
Rhaphanocrinus	Camerata	471.8	443.7	0.13	65.0
Rhenocrinus	Cladida	411.2	397.5	0.38	96.0
Rhipidocrinus	Camerata	416	385.3	0.25	49.0
Rhodocrinites	Camerata	416	326.4	0.12	28.0
Rhopocrinus	Cladida	333	318.1	0.08	54.0
Schistocrinus	Cladida	318.1	299	0.14	18.5
Scotiacrinus	Cladida	345.3	315	0.13	71.5
Scytalocrinus	Cladida	374.5	299	0.27	60.0
Sellardsicrinus	Cladida	308	306.5	0.13	45.0
Sostronocrinus	Cladida	374.5	348	0.21	30.6
Springeracrocrinus	Camerata	359.2	318.1	0.19	18.0
Spyridiocrinus	Camerata	416	397.5	0.06	1.0
Stachyocrinus	Cladida	299	251	0.30	20.0
Stelidiocrinus	Camerata	488.3	422.9	0.25	13.3
Sunwaptacrinus	Camerata	359.2	340	0.10	28.7
Synbathocrinus	Disparida	416	251	0.50	46.0
Taxocrinus	Flexibilia	397.5	318.1	0.14	81.0
Technocrinus	Camerata	438	407	0.13	65.0
Teleiocrinus	Camerata	348	340	0.04	50.0
Texacrinus	Cladida	359.2	280	0.18	35.3
Thylacocrinus	Camerata	416	385.3	0.08	42.0
Triacrinus	Disparida	428.2	422.9	0.50	141.3
Trichinocrinus	Camerata	471.8	464	0.25	11.2
Tundracrinus	Cladida	308	275.6	0.12	48.0
Tunguskocrinus	Disparida	471.8	460.9	0.39	15.4
Ulocrinus	Cladida	311.7	299	0.29	100.0
Ulrichicrinus	Cladida	348	306.5	0.14	79.0
Woodocrinus	Cladida	359.2	251	0.15	71.0
Xenocrinus	Camerata	451	443.7	0.17	1.0
Zeacrinites	Cladida	359.2	305	0.12	69.0

Appendix B: Comparison of EAL data under different time divisions

Line marked “modified” (black) indicates ICS epoch-level divisions subdivided by ages where necessary to approximate even-length bins; these were the boundaries used in deriving all results presented in Chapter III. Error bars indicate 1 bootstrapped standard deviation.



Appendix C: Alternative method for estimating spine regeneration frequency

A simple average-based method for estimating true regeneration frequency (R_{true}) in structures with a fixed maximum length (L_{max}) was presented in Chapter IV. Briefly, if postmortem breakage were to result in the loss of the regenerating tip, regeneration would not be observed for that spine; this means that the observed regeneration frequency R_{obs} is an underestimate. This section presents an alternative method based on observed lengths.

1) As in the method in Chapter IV, the ratio of length to the square root of (width × depth) at the base was calculated for all unbroken specimens of each anatomical type. This value was then used to estimate the maximum lengths (L_{max}) of all broken specimens from their base measurements.
2) For actual regeneration frequencies (R_t) ranging from 1% to 20%, simulated regeneration frequencies were modeled by choosing R_t*n of the specimens. The L_{max} for each of those specimens was multiplied by a value between 0 and 1 to give a simulated regeneration length, L_{sim}. Both a uniform distribution on (0,1) and a truncated Gaussian with
3) Actual observed length, L_{obs}, was superimposed over L_{sim} for all spines to give a simulated apparent regeneration frequency. If $L_{obs}>L_{sim}$ and $L_{sim}<L_{max}$, the spine was marked as "observed regenerating"; if $L_{obs}\leq L_{sim}$ or $L_{sim}=L_{max}$, no regeneration was observed. A value for R_{obs} was thus obtained for each value of R_t.
4) The value of R_t for which R_{obs} coincided with the regeneration frequency observed in the real sample was taken as the best estimate of true regeneration frequency for the sample.

The values for the Pennsylvanian through Permian sample of poteriocrines are compared below. Note that only one cup spine from the Upper Pennsylvanian was regenerating and therefore no normal distribution could be estimated.

Age	Type	n	Obs. regen. freq. (%)	Est. true regen. freq. (%) by method in Ch. IV	Est. true regen. freq. (%) by this method, uniform distribution	Est. true regen. freq. (%) by this method, normal distribution
All	Anal sac	430	4.9	6.2	**6.3**	**8.1**
	Cup	748	7.9	9.4	**9.5**	**11.3**
M. Penn	Anal sac	54	3.7	4.2	**4.3**	**5.9**
	Cup	460	10.0	12.0	**11.9**	**14.4**
U. Penn	Anal sac	211	7.6	9.9	**10**	**14.1**
	Cup	12	8.3	14.5	**14.2**	---
L. Perm	Anal sac	157	1.9	2.4	**2.5**	**2.7**
	Cup	232	4.7	5.6	**5.9**	**6.2**

Temporal and anatomical patterns in estimated regeneration frequencies are consistent regardless of the method: anal sac spines < first primibrach (cup) spines and Upper Pennsylvanian > Middle Pennsylvanian > Lower Permian. For all groups, the ranking of the four regeneration frequencies is the same: The normal distribution results in slightly higher estimates than the uniform distribution, which is in turn slightly higher than the average-based method, which is higher than the observed regeneration frequency. The average-based method, as the most conservative estimate, is used in the text of Chapter IV.

BIBLIOGRAPHY

Bibliography

Algeo, T. J., and P. H. Heckel. 2008: The Late Pennsylvanian Midcontinent Sea of North America: a review. Palaeogeography, Palaeoclimatology, Palaeoecology 268:205–221.

Amemiya, S., and T. Oji. 1992: Regeneration in sea lilies. Nature 357:546–547.

Améziane-Cominardi, N. 1999: Les genres *Cyathidium* et *Holopus* au sein des Cyrtocrinida (Crinoidea; Echinodermata). Journal of Natural History 33.

Améziane-Cominardi, N., Bourseau, Jean-Paul, R. Avocat, and M. Roux. 1990: Les crinoïdes pédonculés de Nouvelle Calédonie: inventaire et réflexions sur les taxons archaïques. Pp.117–124 *in* M. Jangoux, C. De Ridder, P. Dubois, and M.-C. Lahaye, eds. Echinoderm Research. Balkema, Rotterdam.

Améziane, N., and M. Roux. 1997: Biodiversity and historical biogeography of stalked crinoids (Echinodermata) in the deep sea. Biodiversity & Conservation 6:1557–1570.

Aronson, R. B. 1991a: Escalating predation on crinoids in the Devonian: negative community-level evidence. Lethaia 24:123–128.

Aronson, R. B. 1991b: Predation, physical disturbance, and sublethal arm damage in ophiuroids: a Jurassic-Recent comparison. Marine Ecology Press Series 74:91–97.

Ausich, W. I. 1980: A Model for Niche Differentiation in Lower Mississippian Crinoid Communities. Journal of Paleontology 54:273–288.

——— 1988: Evolutionary Convergence and Parallelism in Crinoid Calyx Design. Journal of Paleontology 62:906–916.

——— 1997: Calyx plate homologies and early evolutionary history of the Crinoidea. *in* Geobiology of Echinoderms. The Paleontological Society Papers, 3, 289-304.

Ausich, W. I., and E. W. Roeser. 2012: Camerate and Disparid Crinoids from the Late Kinderhookian Meadville Shale, Cuyahoga Formation of Ohio. Journal of Paleontology 86:488–507.

Ausich, W. I., T. W. Kammer, and T. K. Baumiller. 1994: Demise of the Middle Paleozoic Crinoid Fauna: A Single Extinction Event or Rapid Faunal Turnover? Paleobiology 20:345–361.

Ausich, W. I., T. W. Kammer, and L. C. Sallan. 2011: Climate change versus predation: drivers for macroevolutionary transitions within Paleozoic crinoids. Geological Society of America Abstracts with Programs 43 (5):503.

Ausich, W. I., P. Copper, Canadian Society of Petroleum Geologists., and Geological Association of Canada. 2010: The Crinoidea of Anticosti Island, Québec (late Ordovician to early Silurian). *in* Palaeontographica Canadiana,0821-7556 ;no. 29. Canadian Society of Petroleum Geologists, Calgary.

Bambach, R. K. 1993: Seafood Through Time: Changes in Biomass, Energetics, and Productivity in the Marine Ecosystem. Paleobiology 19:372–397.

——— 1999: Energetics in the global marine fauna: A connection between terrestrial diversification and change in the marine biosphere. Geobios 32:131–144.

——— 2002: Supporting predators: changes in the global ecosystem inferred from changes in predator diversity. Paleontological Society Papers 8:319–352.

Baumiller, T. K. 1990: Non-predatory drilling of Mississippian crinoids by platyceratid gastropods. Paleobiology 33:743–748.

——— 1993: Survivorship analysis of Paleozoic Crinoidea: effect of filter morphology on evolutionary rates. Paleobiology 19:304–321.

——— 2003a: Experimental and biostratinomic disarticulation of crinoids: taphonomic implications. Pp.243–248 *in* J. P. Feral and B. David, eds. Echinoderm Research 2001. Balkema, Rotterdam.

Baumiller, T. K. 2003b: Evaluating the interaction between platyceratid gastropods and crinoids: a cost–benefit approach. Palaeogeography, Palaeoclimatology, Palaeoecology 201:199–209.

Baumiller, T. K. 2008: Crinoid Ecological Morphology. Annual Review of Earth and Planetary Sciences 36:221–249.

——— 2013a: Ephemeral injuries, regeneration frequencies, and intensity of the injury-producing process. Marine Biology 160:3233–3239.

——— 2013b: Arm regeneration frequencies in Florometra serratissima (Crinoidea, Echinodermata): impact of depth of habitat on rates of arm loss. Cahiers de Biologie Marine 54:571–576.

Baumiller, T. K., and W. I. Ausich. 1992: The broken-stick model as a null hypothesis for crinoid stalk taphonomy and as a guide to the distribution of connective tissue in fossils. Paleobiology 18:288–298.

Baumiller, T. K., and A. Gaździcki. 1996: New crinoids from the Eocene La Meseta Formation of Seymour Island, Antarctic Peninsula. Pp.101–116 *in* A. Gaździcki, ed. Palaeontological Results of the Polish Antarctic Expedition. II. .

Baumiller, T. K., and F. J. Gahn. 2002: Fossil record of parasitism on marine invertebrates with special emphasis on the platyceratid-crinoid interaction. Pp.195–210 *in* M. Kowalewski and P. H. Kelley, eds. The Fossil Record of Predation. Paleontological Society.

——— 2004: Testing predator-driven evolution with Paleozoic crinoid arm regeneration. Science 305:1453–1455.

——— 2013: Reconstructing predation pressure on crinoids: estimating arm-loss rates from regenerating arms. Paleobiology 39:40–51.

Baumiller, T. K., F. J. Gahn, and J. Savill. 2004: New data and interpretations of the crinoid-platyceratid interaction. Pp. 393-398 *in* Echinoderms: Muenchen. Taylor & Francis Group, London.

Baumiller, T. K., R. Mooi, and C. G. Messing. 2008: Urchins in the meadow: paleobiological and evolutionary implications of cidaroid predation on crinoids. Paleobiology 34:22–34.

Baumiller, T. K., M. A. Salamon, P. Gorzelak, R. Mooi, C. G. Messing, and F. J. Gahn. 2010: Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution. Proceedings of the National Academy of Sciences 107:5893–5896.

Berner, R. A. 2006: GEOCARBSULF: A combined model for Phanerozoic atmospheric O2 and CO2. Geochimica et Cosmochimica Acta 70:5653–5664.

Bottjer, D. J., and D. Jablonski. 1988: Paleoenvironmental patterns in the evolution of post-Paleozoic benthic marine invertebrates. PALAIOS 3:540-560.

Brett, C. E. 2003: Durophagous predation in Paleozoic marine benthic assemblages. Pp.401–432 *in* P. H. Kelley, M. Kowalewski, and T. A. Hansen, eds. Predator—Prey Interactions in the Fossil Record. Springer US, New York.

Brett, C. E., and S. E. Walker. 2002: Predators and predation in Paleozoic marine environments. Pp.93–118 *in* M. Kowalewski and P. H. Kelley, eds. The Fossil Record of Predation. Vol. 8. Paleontological Society.

Brett, C. E., W. I. Ausich, and M. J. Simms. 2003: Fossil Crinoids. Cambridge University Press, New York.

Brett, C. E., F. J. Gahn, and T. K. Baumiller. 2004: Platyceratid gastropods as parasites, predators, and prey and their possible effects on echinoderm hosts: collateral damage and targeting. Geological Society of America Abstracts with Programs 36:478.

Brower, J. C. 2006: Ontogeny of the food-gathering system in Ordovician crinoids. Journal of Paleontology 80:430–446.

Bush, A. M., R. K. Bambach, and G. M. Daley. 2007: Changes in theoretical ecospace utilization in marine fossil assemblages between the Mid-Paleozoic and Late Cenozoic. Paleobiology 33:76–97.

Carnevali, M. D. C., E. Lucca, and F. Bonasoro. 1993: Mechanisms of arm regeneration in the feather star *Antedon mediterranea*: Healing of wound and early stages of development. Journal of Experimental Zoology 267:299–317.

Carpenter, P. H. 1884: Report upon the Crinoidea collected during the voyage of H.M.S. Challenger during the years 1873-76. Part I: General morphology, with descriptions of the stalked crinoids. *in* Reports on the Scientific Results of the Voyage of H. M. S. Challenger. Part V: Zoology. Vol. 32. Smithsonian Institution.

Charbonnier, S., J. Vannier, C. Gaillard, J.-P. Bourseau, and P. Hantzpergue. 2007: The La Voulte Lagerstätte (Callovian): Evidence for a deep water setting from sponge and crinoid communities. Palaeogeography, Palaeoclimatology, Palaeoecology 250:216–236.

Conway Morris, S. 1981: Parasites and the fossil record. Parasitology 82:489–509.

Cowen, R. 1981: Crinoid arms and banana plantations: an economic harvesting analogy. Paleobiology 7:332–343.

Dahl, T. 2010: Devonian rise in atmospheric oxygen correlated to the radiations of terrestrial plants and large predatory fish. PNAS 107:17911–17915.

Davies, T. T., M. A. Crenshaw, and B. M. Heatfield. 1972: The effect of temperature on the chemistry and structure of echinoid spine regeneration. Journal of Paleontology 46:874–883.

Dietl, G. P. 2003: The escalation hypothesis: one long argument. PALAIOS 18:83–86.

Donovan, S. K. 1990: Functional morphology of synostosial articulations in the crinoid column. Lethaia 23:291–296.

——— 1992: Scanning EM study of the living cyrtocrinid *Holopus rangii* (Echinodermata, Crinoidea) and implications for its functional morphology. Journal of Paleontology 66:665–675.

——— 2012: Was autotomy a pervasive adaptation of the crinoid stalk during the Paleozoic? Geology 40(10):867-870.

Donovan, S. K., and S. Jakobsen. 2004: An unusual crinoid-barnacle association in the type area of the Danian (Paleocene), Denmark. Lethaia 37:407–415.

Donovan, S. K., and D. L. Pawson. 2008: A new species of the sessile crinoid *Holopus* d'Orbigny from the tropical western Atlantic, with comments on holopodid ecology (Echinodermata: Crinoidea: Holopodidae). Zootaxa 1717:31–38.

Duco, A., and M. Roux. 1981: Modalités particulières de croissance liées au milieu abyssal chez les Bathycrinidae (Echinodermes, Crinoïdes pédonculés). Oceanologica Acta 4:389–394.

Emson, R. H., P. V. Mladenov, and K. Barrow. 1991: The feeding mechanism of the basket star *Gorgonocephalus arcticus*. Canadian Journal of Zoology 69:449–455.

Fishelson, L. 1974: Ecology of the northern Red Sea crinoids and their epi- and endozoic fauna. Marine Biology 26:183–192.

Foote, M. 1999: Morphological diversity in the evolutionary radiation of Paleozoic and post-Paleozoic crinoids. Paleobiology 25:1–116.

Gahn, F. J., and T. K. Baumiller. 2001: Testing evolutionary escalation between crinoids and platyceratid gastropods and phylogenetic analysis of the Compsocrinina (Crinoidea: Monobathrida). Geological Society of America Abstracts with Programs 33(6):247.

——— 2003: Infestation of Middle Devonian (Givetian) camerate crinoids by platyceratid gastropods and its implications for the nature of their biotic interaction. Lethaia 36:71–82.

——— 2005: Arm regeneration in Mississippian crinoids: evidence of intense predation pressure in the Paleozoic? Paleobiology 31:151–164.

——— 2006: Using platyceratid gastropod behaviour to test functional morphology. Historical Biology 18:397–404.

——— 2010: Evolutionary history of regeneration in crinoids (Echinodermata). Integrative and Comparative Biology 50:514a – 514m.

Gorzelak, P., M. A. Salamon, and T. K. Baumiller. 2012: Predator-induced macroevolutionary trends in Mesozoic crinoids. Proceedings of the National Academy of Sciences 109:7004–7007.

Gorzelak, P., E. Głuchowski, and M. A. Salamon. 2014: Reassessing the improbability of a muscular crinoid stem. Scientific Reports 4:6019.

Gorzelak, P. L., L. Rakowicz, M. A. Salamon, and P. Szrek. 2011: Inferred placoderm bite marks on Devonian crinoids from Poland. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 259:105–112.

Greene, S. E., D. J. Bottjer, and J.-P. Zonneveld. 2012: Timing the twilight of the crinoids: when did crinoids cede ecological dominance? Geological Society of America Abstracts with Programs.

Grimmer, J. C., and N. D. Holland. 1990: The structure of a sessile, stalkless crinoid (*Holopus rangii*). Acta Zoologica 71:61–67.

Hagdorn, H. 2011: Triassic: the crucial period of post-Palaeozoic crinoid diversification. Swiss Journal of Palaeontology 130:91–112.

Heinzeller, T., and H. Fechter. 1995: Microscopical anatomy of the cyrtocrinid *Cyathidium meteorensis* (sive *foresti*) (Echinodermata, Crinoidea). Acta Zoologica 76:25–34.

Hempson, T. N., and C. L. Griffiths. 2008: Symbionts of comatulid crinoids in False Bay, South Africa. African Zoology 43:237–244.

Hess, H. 2006: Crinoids (Echinodermata) from the Lower Jurassic (Upper Pliensbachian) of Arzo, Southern Switzerland. *in* Schweizerische paläontologische Abhandlungen. Vol. 126. Kommission der Schweizerischen Paläontologischen Abhandlungen, Basel, p.

——— 2014: The crinoid *Eugeniacrinites cariophilites* from the Late Jurassic of southern Germany: babies, cripples and enigmatic wing plates. Swiss Journal of Palaeontology 133.

Hess, H., C. G. Messing, and W. I. Ausich. 2011: Crinoidea 3. Articulata. Pp.1–261 *in* Part T. Echinodermata 2: Crinoidea. University of Kansas Paleontological Institute, Lawrence, Kansas.

House, M. R. 2002: Strength, timing, setting and cause of mid-Palaeozoic extinctions. Palaeogeography, Palaeoclimatology, Palaeoecology 181:5–25.

Huntley, J. W., and M. Kowalewski. 2007: Strong coupling of predation intensity and diversity in the Phanerozoic fossil record. Proceedings of the National Academy of Sciences 104:15006–15010.

Janevski, G. A. 2011: Causes and consequences of extinction and survival in fossil marine invertebrates with a special focus on the Crinoidea (Phylum Echinodermata). Ph.D., University of Michigan, Ann Arbor, 192pp.

Janevski, G. A., and T. K. Baumiller. 2010: Could a stalked crinoid swim? A biomechanical model and characteristics of swimming crinoids. PALAIOS 25:588–596.

Kammer, T. W., and W. I. Ausich. 1987: Aerosol suspension feeding and current velocities: distributional controls for Late Osagean crinoids. Paleobiology 13:379–395.

——— 2006: The "Age of Crinoids": a Mississippian biodiversity spike coincident with widespread carbonate ramps. Palaios 21:238–248.

Kemami Wangun, H. V., A. Wood, C. Fiorilla, J. K. Reed, P. J. McCarthy, and A. E. Wright. 2010: Gymnochromes E and F, cytotoxic phenanthroperylenequinones from a deep-water crinoid, *Holopus rangii*. Journal of Natural Products 73:712–715.

Kesling, R. V. 1965: Nature and occurrence of *Gennaeocrinus goldringae* Ehlers. Contributions from the University of Michigan Museum of Paleontology XIX:265–280.

Klug, C., B. Kröger, W. Kiessling, G. L. Mullins, T. Servais, J. Frýda, D. Korn, and S. Turner. 2010: The Devonian nekton revolution. Lethaia 43:465–477.

Kröger, B. 2005: Adaptive evolution in Paleozoic coiled cephalopods. Paleobiology 31:253–268.

Lamsdell, J. C., and S. J. Braddy. 2009: Cope's rule and Romer's theory: patterns of diversity and gigantism in eurypterids and Palaeozoic vertebrates. Biology Letters.

Lane, N. G. 1984: Predation and survival among inadunate crinoids. Paleobiology 10:453–458.

Lawrence, J. M. 2009: Arm loss and regeneration in stellate echinoderms: an organismal view. Pp.53–66 *in* C. Johnson, ed. Echinoderms in a Changing World: Proceedings of the 13th International Echinoderm Conference. Hobart, Tasmania, Australia.

Lawrence, J. M., and J. Vasquez. 1996: The effect of sublethal predation on the biology of echinoderms. Oceanologica Acta 19:431–440.

Lindsay, S. M. 2010: Frequency of injury and the ecology of regeneration in marine benthic invertebrates. Integrative and Comparative Biology 50:479–493.

Long, J. A. 1995: The rise of fishes: 500 million years of evolution. Johns Hopkins University Press, Baltimore, p.

Macurda, D. B. 1976: Skeletal modifications related to food capture and feeding behavior of the basketstar *Astrophyton*. Paleobiology 2:1–7.

McClintock, J. B., B. J. Baker, T. K. Baumiller, and C. G. Messing. 1999: Lack of chemical defense in two species of stalked crinoids: support for the predation hypothesis for Mesozoic bathymetric restriction. Journal of Experimental Marine Biology and Ecology 232:1–7.

Messier, C., R. Doucet, J.-C. Ruel, Y. Claveau, C. Kelly, and M. J. Lechowicz. 1999: Functional ecology of advance regeneration in relation to light in boreal forests. Canadian Journal of Forest Research 29:812–823.

Messing, C. G., J. David, M. Roux, N. Améziane, and T. K. Baumiller. 2007: In situ stalk growth rates in tropical western Atlantic sea lilies (Echinodermata: Crinoidea). Journal of Experimental Marine Biology and Ecology 353:211–220.

Meyer, D. L. 1985: Evolutionary implications of predation on recent comatulid crinoids from the Great Barrier Reef. Paleobiology 11:154–164.

Meyer, D. L., and D. B. Macurda. 1977: Adaptive radiation of the comatulid crinoids. Paleobiology 3:74–82.

Meyer, D. L., and W. I. Ausich. 1983: Biotic interactions among recent and among fossil crinoids. Pp.377–427 *in* M. J. S. Tevesz and P. L. McCall, eds. Biotic Interactions in Recent and Fossil Benthic Communities. Plenum Press, New York.

Meyer, D. L., C. A. LaHaye, N. D. Holland, A. C. Arneson, and J. R. Strickler. 1984: Time-lapse cinematography of feather stars (Echinodermata: Crinoidea) on the Great Barrier Reef, Australia: demonstrations of posture changes, locomotion, spawning and possible predation by fish. Marine Biology 78:179–184.

Mladenov, P. V. 1983: Rate of arm regeneration and potential causes of arm loss in the feather star *Florometra serratissima* (Echinodermata: Crinoidea). Canadian Journal of Zoology 61:2873–2879.

Moore, R. C., and R. M. Jeffords. 1967: Stratigraphic usefulness of crinoid fragments. Esso Production Research Company, Stratigraphic Geology Division, Houston.

Moore, R., H. W. Rasmussen, N. G. Lane, G. Ubaghs, H. L. Strimple, R. E. Peck, J. Sprinkle, R. O. Fay, and H. Sieverts-Doreck. 1978: Crinoidea 2. Systematic Descriptions. Pp.T403–T812 *in* Part T. Echinodermata 2: Crinoidea. Geological Society of America and University of Kansas, Boulder, Colorado; Lawrence, Kansas.

Nichols, D. 1994: Reproductive seasonality in the comatulid crinoid *Antedon bifida* (Pennant) from the English Channel. Philosophical Transactions of the Royal Society B: Biological Sciences 343:113–134.

Novack-Gottshall, P. M. 2008: Using simple body-size metrics to estimate fossil body volume: empirical validation using diverse Paleozoic invertebrates. PALAIOS 23:163–173.

O’Malley, C. E., W. I. Ausich, and Y.-P. Chin. 2013: Isolation and characterization of the earliest taxon-specific organic molecules (Mississippian, Crinoidea). Geology 41:347–350.

Oji, T. 1989: Growth rate of stalk of *Metacrinus rotundus* (Echinodermata: Crinoidea) and its functional significance. J. Fac. Sci. Univ. Tokyo 22:39–51.

——— 1996: Is predation intensity reduced with increasing depth? Evidence from the West Atlantic stalked crinoid *Endoxocrinus parrae* (Gervais) and implications for the Mesozoic Marine Revolution. Paleobiology 22:339–351.

——— 2001: Fossil record of echinoderm regeneration with special regard to crinoids. Microscopy Research and Technique 55:397–402.

Oji, T., and T. Okamoto. 1994: Arm autotomy and arm branching pattern as anti-predatory adaptations in stalked and stalkless crinoids. Paleobiology 20:27–39.

Payne, J. L., A. G. Boyer, J. H. Brown, S. Finnegan, M. Kowalewski, R. A. Krause, S. K. Lyons, C. R. McClain, D. W. McShea, P. M. Novack-Gottshall, F. A. Smith, J. A. Stempien, and S. C. Wang. 2009: Two-phase increase in the maximum size of life over 3.5 billion years reflects biological innovation and environmental opportunity. Proceedings of the National Academy of Sciences 106:24–27.

Peters, S. E., and W. I. Ausich. 2008: A sampling-adjusted macroevolutionary history for Ordovician–Early Silurian crinoids. Paleobiology 34:104–116.

R Core Team. 2014: R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rideout, J. A., N. B. Smith, and M. D. Sutherland. 1979: Chemical defense of crinoids by polyketide sulphates. Experientia 35:1273–1274.

Rollins, H. B., and D. K. Brezinski. 1988: Reinterpretation of crinoid-platyceratid interaction. Lethaia 21:207–217.

Rosenberg, R., S. Dupont, T. Lundälv, H. N. Sköld, A. Norkko, J. Roth, T. Stach, and M. Thorndyke. 2005: Biology of the basket star *Gorgonocephalus caputmedusae* (L.). Marine Biology 148:43–50.

Rouse, G. W., L. S. Jermiin, N. G. Wilson, I. Eeckhaut, D. Lanterbecq, T. Oji, C. M. Young, T. Browning, P. Cisternas, L. E. Helgen, M. Stuckey, and C. G. Messing. 2013: Fixed, free, and fixed: The fickle phylogeny of extant Crinoidea (Echinodermata) and their Permian–Triassic origin. Molecular Phylogenetics and Evolution 66:161–181.

Roux, M. 1976: Aspects de la variabilité et de la croissance au sein d'une population de la pentacrine actuelle: *Annacrinus wyvillethomsoni* Jeffreys (Crinoidea). Thallas. Jugosl. 12:307–320.

Salamon, M. A., and P. Gorzelak. 2007: Evidence of shallow-water cyrtocrinids (Crinoidea) from the Callovian of Poland. Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen 244:257–260.

——— 2011: A new spoon-like crinoid (*Hemicrinus*, Cyrtocrinida) from the Danian (Palaeogene) of Poland and overview of Cretaceous hemicrinids. Paleontological Research 15:23–30.

Salamon, M. A., P. Gorzelak, and M. Zatoń. 2009: In quest of cyrtocrinid origins: evidence from Late Triassic ossicles from the Tatra Mountains. Acta Palaeontologica Polonica 54:171–174.

Salamon, M. A., P. Gorzelak, R. Niedźwiedzki, D. Trzęsiok, and T. K. Baumiller. 2014: Trends in shell fragmentation as evidence of mid-Paleozoic changes in marine predation. Paleobiology 40:1–10.

Sallan, L. C. 2013: The end-Devonian Hangenberg event: causes and consequences of a major bottleneck in vertebrate evolution. Geological Society of America Abstracts with Programs 45:7:319.

Sallan, L. C., and M. I. Coates. 2010: End-Devonian extinction and a bottleneck in the early evolution of modern jawed vertebrates. Proceedings of the National Academy of Sciences 107:10131–10135.

Sallan, L. C., T. W. Kammer, W. I. Ausich, and L. A. Cook. 2011: Persistent predator–prey dynamics revealed by mass extinction. Proceedings of the National Academy of Sciences 108:8335–8338.

Schneider, C. L. 2001: Heaps of echinoids in a Pennsylvanian echinoderm Lagerstätte: implications for fossilized behavior. Paleobios 21 (2):113.

Schneider, J. A. 1988: Frequency of arm regeneration of comatulid crinoids in relation to life habit. Pp.531–538 *in* Echinoderm Biology (Proceedings of the Sixth International Echinoderm Conference). Balkema, Rotterdam.

Seilacher, A., and R. B. Hauff. 2004: Constructional morphology of pelagic crinoids. PALAIOS 19:3–16.

Servais, T., A. W. Owen, D. A. T. Harper, B. Kröger, and A. Munnecke. 2010: The Great Ordovician Biodiversification Event (GOBE): The palaeoecological dimension. Palaeogeography, Palaeoclimatology, Palaeoecology 294:99–119.

Signor, P. W., and C. E. Brett. 1984: The Mid-Paleozoic precursor to the Mesozoic Marine Revolution. Paleobiology 10:229–245.

Simpson, C. 2010: Species selection and driven mechanisms jointly generate a large-scale morphological trend in monobathrid crinoids. Paleobiology 36:481–496.

Springer, F. 1920: The Crinoidea flexibilia : (with an atlas of A., B., C., and 76 plates). *in* Publications of the Smithsonian Institute. Smithsonian Institution, Washington, D.C., p.

Syverson, V. J., and T. K. Baumiller. 2014: Temporal trends of predation resistance in Paleozoic crinoid arm branching morphologies. Paleobiology 40:417–427.

Ubaghs, G., A. Breimer, N. G. Lane, H. W. Rasmussen, R. C. Moore, J. C. Brower, H. Sieverts-Doreck, H. L. Strimple, and D. B. Macurda. 1978: Crinoidea 1. General Features of Crinoidea. Pp.T1–T402 *in* Part T. Echinodermata 2: Crinoidea. Geological Society of America and University of Kansas, Boulder, Colorado; Lawrence, Kansas.

Vermeij, G. J. 1977: The Mesozoic Marine Revolution: evidence from snails, predators and grazers. Paleobiology 3:245–258.

Vermeij, G. J. 1987: Evolution and escalation : an ecological history of life. Princeton Univ Press, Princeton.

Vermeij, G. J. 2002: Evolution in the consumer age: predators and the history of life. Pp.375–394 *in* M. Kowalewski and P. H. Kelley, eds. Predation in the Fossil Record. Paleontological Society.

——— 2013: On escalation. Annual Review of Earth and Planetary Sciences 41.

Wachsmuth, C., and F. Springer. 1897: The North American Crinoidea camerata. *in Memoirs of the Museum of Comparative Zoology at Harvard College*. Vol. 20.–21. Harvard Museum of Comparative Zoology, Cambridge, U.S.A.

Waters, J. A., and C. G. Maples. 1991: Mississippian Pelmatozoan community reorganization: a predation-mediated faunal change. Paleobiology 17:400–410.

Webby, B. D., F. Paris, M. L. Droser, and I. G. Percival. 2004: The Great Ordovician Biodiversification Event. Columbia University Press, New York.

Webster, G. D. 2003: Bibliography and index of Paleozoic crinoids, coronates, and hemistreptocrinoids, 1758–2012. *in Geological Society of America Special Papers*. Vol. 363. Boulder, Colorado, p.

Webster, G. D., R. T. Becker, and C. G. Maples. 2005: Biostratigraphy, paleoecology, and taxonomy of Devonian (Emsian and Famennian) crinoids from Southeastern Morocco. Journal of Paleontology 79:1052–1071.

Wisshak, M., C. Neumann, J. Jakobsen, and A. Freiwald. 2009: The “living-fossil community” of the cyrtocrinid *Cyathidium foresti* and the deep-sea oyster *Neopycnodonte zibrowii* (Azores Archipelago). Palaeogeography, Palaeoclimatology, Palaeoecology 271:77–83.

Wolkenstein, K., J. H. Gross, H. Falk, and H. F. Schöler. 2006: Preservation of hypericin and related polycyclic quinone pigments in fossil crinoids. Proceedings of the Royal Society B: Biological Sciences 273:451–456.