Persistent predator–prey dynamics revealed by mass extinction

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Predator–prey interactions are thought by many researchers to define both modern ecosystems and past macroevolutionary events. In modern ecosystems, experimental removal or addition of taxa is often used to determine trophic relationships and predator identity. Both characteristics are notoriously difficult to infer in the fossil record, where evidence of predation is usually limited to damage from failed attacks, individual stomach contents, one-sided escalation, or modern analogs. As a result, the role of predation in macroevolution is often dismissed in favor of competition and abiotic factors. Here we show that the end-Devonian Hangenberg event (359 Mya) was a natural experiment in which vertebrate predators were both removed and added to an otherwise stable prey fauna, revealing specific and persistent trophic interactions. Despite apparently favorable environmental conditions, crinoids diversified only after removal of their vertebrate consumers, exhibiting predatory release on a geological time scale. In contrast, later Mississippian (359–318 Mya) camerate crinoids declined precipitously in the face of increasing predation pressure from new durophagous fishes. Camerate failure is linked to the retention of obsolete defenses or "legacy adaptations" that prevented coevolutionary escalation. Our results suggest that major crinoid evolutionary phenomena, including rapid diversification, faunal turnover, and species selection, might be linked to vertebrate predation. Thus, interactions observed in small ecosystems, such as Lotka-Volterra cycles and trophic cascades, could operate at geologic time scales and higher taxonomic ranks. Both trophic knock-on effects and retention of obsolete traits might be common in the aftermath of predator extinction.

Carboniferous | durophagy | biodiversity | paleontology | macroecology

Predator–prey interactions are thought by many researchers to underpin major evolutionary events, yet they are notoriously difficult to define in the fossil record (1–4). Predator identity inferred from diagnostic marks (e.g., gastropod boring scars), stomach contents, or recent observations gives little indication of pervasiveness (3, 5). Large-scale predation pressure inferred from escalation of, or persistent damage to, prey defenses reveals little about specific relationships and might not reflect real trends (3, 4, 6). Predation effects can be hard to distinguish from those of competition and abiotic changes (1). As a result, predation has been underrated as a driver of biodiversity and faunal composition (1).

In living ecosystems, trophic interactions are teased apart via experimental manipulations, such as removal and introduction of consumers (7). These produce trophic cascades or other Lotka-Volterra processes, whereby prey numbers change in opposition to predator demographics, and vice versa (8). Larger-scale diversity might be prone to the same phenomena because speciation and extinction can be linked to population size (9). In addition, prey diversity is known to be impacted by predator introduction in small-scale ecosystems (7). A macroevolutionary equivalent of ecological manipulation would be an extinction predominantly affecting a single trophic level.

The end-Devonian Hangenberg event (359 Mya) provides a natural experiment in which potential predators are both re-moved (via extinction) and introduced (in the form of unspecialized survivors) to a prey biota with stable diversity trends (10–13). During the Mid-Paleozoic Marine Revolution (MPMR), crinoids and other benthic invertebrates exhibited signs of escalation, including greater armature and spinosity (2, 6, 14). This has been linked to increased predation from nektonic ammonoids, arthropods, and especially jawed vertebrates—all devastated by the Hangenberg extinction (6, 10, 11, 15–17). Among vertebrates, a number of unique novel fish lineages appeared in the postextinction Mississippian subsystem of the Carboniferous period (11).

Crinoid faunas passed through the Hangenberg event relatively unscathed, exhibiting little turnover at the Devonian–Mississippian boundary (359 Mya). Crinoids were also unaffected by the earlier Frasnian–Famennian Kellwasser extinction of marine invertebrates (374 Mya) (13). Instead, the largest crinoid mass extinction of the mid-Paleozoic took place at the even earlier Givetian–Frasnian boundary, resulting in a reduction of crinoid generic diversity by approximately one third (18) (Fig. 1 and *SI Appendix*, Table S1). However, by the Famennian, diversity had only recovered to the same level as present in the Givetian (*SI Appendix*, Table S1). Thus, the Frasnian–Mississippian crinoid record provides the stable prey biota required for our natural experiment.

In addition, Mississippian crinoids exhibited two common diversity trends traditionally attributed to similar environmental and/or competitive factors (1, 12, 19). The first was a diversification climax starting in the Tournaisian stage (359–345 Mya), establishing an "Age of Crinoids" evidenced by widespread encrinital limestones (12). The second was faunal turnover in the later Mississippian (345–318 Mya), as increased extinction rates for camerate crinoids resulted in the advanced cladid-dominated late Paleozoic evolutionary fauna (5, 12, 19).

Predation has been raised as a possible driver of these crinoid trends but not tested quantitatively (1, 9, 20, 21). It is known that vertebrates did consume crinoids at least intermittently during the Devonian–Carboniferous, on the basis of stomach contents, coprolites, and damage to both crinoids and other benthic invertebrates (12, 17, 22, 23). However, physical evidence for intentional and pervasive predation is limited by a general lack of durophagous fish body fossils with stomach contents. Thus, the vertebrate–crinoid relationship itself is in need of the kind of "experiment" proposed here.

We assembled and compared compendia of the temporal distribution of late Devonian and Mississippian crinoids and durophagous fishes (*SI Appendix, Supporting Methods and Discussion* and Tables S1 and S2). This was done to determine
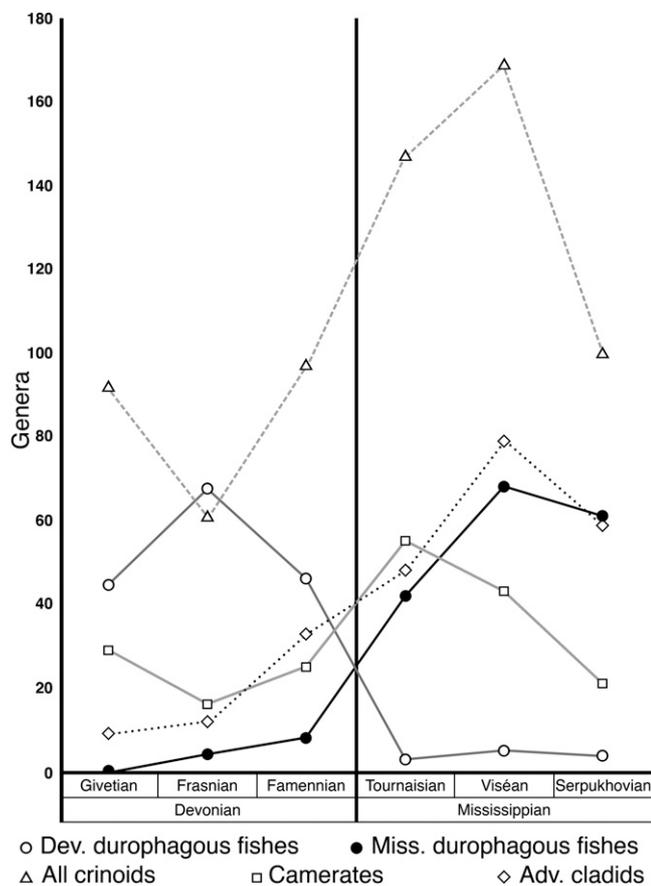
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Fig. 1. Global durophagous vertebrate and crinoid diversity curves (Givetian-Serpukhovian, vertebrate n = 354, crinoid n = 666) (*SI Appendix*, Table S1). Vertical line represents the end-Devonian Hangenberg event (359 Mya).

○ Dev. durophagous fishes ● Miss. durophagous fishes
△ All crinoids □ Camerates ◇ Adv. cladids

whether benthic prey diversity exhibited any reaction to changes in predation pressure near the Hangenberg event and whether predator identity and trophic relationships can be inferred from fossil diversity data. We assume here that taxonomic diversity is a valid proxy for both abundance and predation pressure, a relationship that has been shown previously (4, 17). This assumption also underlies well-known macroevolutionary events such as MPMR and the Mesozoic Marine Revolution, which posit that increased pressure from diversifying predators drove escalation and diversification among benthic invertebrates (2–4, 6, 10). Thus, the comparison of crinoid and vertebrate diversity from the MPMR interval is also a direct test of those phenomena.

Results

Global genera-level diversity curves exhibit both the turnover in durophagous fishes at the Hangenberg extinction and the aforementioned crinoid evolutionary events, including both the early Mississippian peak in diversity and the decline of camerates in the later Mississippian (Fig. 1). Crinoid diversity as a whole is negatively correlated with that of Devonian predators [$r = -0.82$, $P = 0.05$; First Differences (FD) $r = -0.69$ $P = 0.20$] (Fig. 1 and *SI Appendix*, Table S3). The lack of significance in first differencing is due to the drop in crinoid diversity, led by the camerates, in the Serpukhovian. Without the final time slice, the negative relationship between pre-Hangenberg predators and crinoids is much stronger ($r = -0.98$, $P = 0.003$; FD $r = -0.93$ $P = 0.05$) (*SI Appendix*, Table S3) but weakened by the low number of datapoints. However, it is clear that the greatest

increase in Paleozoic crinoid diversity followed the extinction of Devonian predators.

To investigate these patterns further, we divided Mississippian occurrence data from North American and the British Isles into 11 time bins of approximately equal length (*SI Appendix*, Table S2). These two areas have the most comprehensive vertebrate and crinoid records during this interval. Mirrored increases in diversity among Mississippian fish and camerate crinoids during the Tournaisian ($r = 0.96$, $P = 0.04$; FD $r = 0.56$, $P = 0.62$) (Fig. 2 and *SI Appendix*, Table S4) can be attributed to independent radiations after loss of incumbent predators rather than real interaction. The greatest gains among camerate crinoids took place during the Tournaisian stage, during which diversity more than doubled from Late Devonian levels (Fig. 2 and *SI Appendix*, Table S2). This confirms results from the global dataset showing major crinoid diversification as a post-Hangenberg and post-predator extinction phenomenon. The lack of significance in the more conservative first differencing results is not surprising given the small number of data points (three) from the four time intervals (Tournaisian 1–4) available for calculations (4). However, it should be noted that r value remains strongly positive (>0.5) after detrending, which is consistent with the significant correlation observed in the raw data.

Camerates exhibit an abrupt decline beginning at the Tournaisian–Viséan boundary (19, 20, 24). Whereas the overall camerate curve could not be distinguished from a random walk (runs test $P = 0.07$) because of the Tournaisian-Viséan inflection point (Fig. 2 and *SI Appendix, Supporting Methods and Discussion*), the decline could not be directly tested owing to the small number of data points. However, it has long been known that camerates experienced high extinction rates in the later Mississippian and were reduced to just a few lineages by the Pennsylvanian (19, 20, 25). This trend has been attributed to environmental changes favoring advanced cladids (12). Most hypotheses of biotic change without mass extinction also implicate competition, whether direct or indirect (1). However, advanced cladids exhibit a definite random walk pattern indicative of stasis (runs test $P = 0.75$) (Fig. 2), and there is no correlation between the diversity of the two crinoid groups (Tournaisian 1 to Serpukhovian 1: $r = -0.07$, $P = 0.83$; FD $r = -0.41$, $P = 0.27$), even when camerate decline begins in the Viséan (Viséan 1 to Serpukhovian 1: $r = -0.51$, $P = 0.30$; FD $r = 0.47$, $P = 0.43$) (Fig. 2 and *SI Appendix*, Table S4).
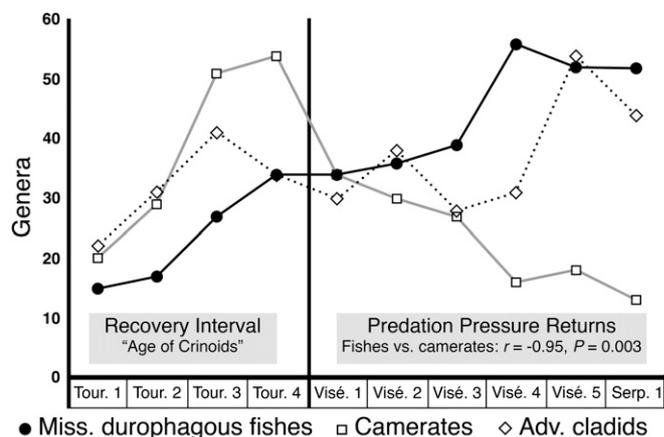

Fig. 2. Post-Hangenberg marine diversity curves for North America and the British Isles (Tournaisian-Serpukhovian, vertebrate n = 416, crinoid n = 671) (*SI Appendix*, Table S2). Vertical line marks the Tournaisian-Viséan boundary (345 Mya).

● Miss. durophagous fishes □ Camerates ◇ Adv. cladids

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In contrast, beginning at the onset of the Viséan, there is a highly significant, strongly negative correlation between the diminishing camerates and a rising diversity of predatory fishes (Fig. 2 and *SI Appendix*, Table S4). Significant increases in durophagous vertebrates (runs test $P = 0.01$) exactly mirror camerate declines from the Viséan through the Serpukhovian (Viséan 1 to Serpukhovian 1: $r = -0.95$, $P = 0.003$; FD $r = -0.89$, $P = 0.04$) (Fig. 2 and *SI Appendix*, Table S4). This relationship held through different interval iterations and cannot be attributed to autocorrelation. In contrast, advanced cladids, our default control group, had an undefined relationship with fishes through the Mississippian (Tournaisian 1 to Serpukhovian 1: $r = 0.55$, $P = 0.10$; FD $r = -0.14$, $P = 0.72$) (Fig. 2 and *SI Appendix*, Table S4). This is the expectation where (*i*) prey were well defended against potential predators, or (*ii*) there is little interaction, and/or (*iii*) nonpredatory factors are also in play (26).

Discussion

The early Mississippian crinoid record might be indicative of large-scale release after predator removal (25). Although the Frasnian–Famennian decimation of platform-edge reefs opened habitat space for crinoids, they were unable to fully use expanded habitats until the Tournaisian (12, 27, 28). The Paleozoic apex of crinoid diversity likely required the separate mass extinction of predatory fishes at the Hangenberg event (Figs. 1 and 2) (11, 12). This pattern of suppression and release supports hypotheses of significant vertebrate–crinoid trophic interaction during the MPMR interval of prey escalation (2, 6, 9). Continued effective predation, in conjunction with environmental factors (13), might have limited crinoid origination and diversity during the Famennian, as shown by the limited occurrences of Famennian taxa, notwithstanding their global rebound to Givetian diversity levels (Fig. 1 and *SI Appendix*, Table S1).

We also conclude that increasing predation pressure from Mississippian predatory fishes contributed to camerate extinctions and turnover of the crinoid evolutionary fauna. The strength of the fish–camerate relationship is shown by signal persistence and the nonrandom directionality of diversity curves for fish and, likely, camerates (*SI Appendix, Supporting Methods and Discussion*). The negative relationship between predator and prey from the same formations, and the decline of camerates in multiple habitats, indicates that the pattern is not primarily driven by environmental change or sampling issues. Large-scale predation could explain much of the fish–crinoid relationship during both the Devonian and Mississippian. The outcome of the Hangenberg "experiment" matches the predictions of modern ecosystem manipulations.

This study cannot address why Mississippian camerate crinoids declined gradually in the face of new predation, a pattern previously hypothesized but not observed quantitatively until now (9). "Red Queen" theory predicts a new arms race during the Viséan (25). Camerate morphology and fish dentitions might provide an explanation. Crinoid defensive structures consist of calcified plates forming a calyx (29). Camerates tended toward greater numbers of small, thickened plates and increased spinosity during the Devonian (6, 20, 24). In contrast, camerates with simplified, unspined calyces made of larger plates were favored in the later Paleozoic (20). The reversal is coincident with a Tournaisian–Viséan inflection point for camerate diversity and has been shown to result at least partially from species-level selection (Fig. 2) (20).

Camerates with complex calyces containing numerous plates (e.g., Actinocrinitidae) evolved 45 new genera in the Tournaisian, 5 in the Visean, and 0 in the Serpukhovian (30–34). Their maximum diversity reached 43 in Tournaisian 4 but fell to 7 genera in Serpukhovian 1 (35). Camerate lineages with simple calyces (arms free above the radials) and containing fewer plates survived (e.g., Platycrinitidae), comprising 6 of the 13 camerates

(46%) in Serpukhovian 1. This is similar to the Famennian, when 11 of 25 camerate genera (44%) had simple calyces (13), perhaps a response to persistent Devonian predators preventing full recovery of benthic prey after the end-Givetian extinction. The Tournaisian proliferation of camerates with complex calyces might have been allowed by the temporary absence of selective predation pressure. As new predators reached critical mass during the Tournaisian–Viséan, complex genera were selectively eliminated, reducing the camerate fauna back to a core of simplified Famennian-like holdovers by the Serpukhovian. The calyx morphologies of camerate survivors were convergent on those primitively exhibited by the more diverse advanced cladids, indicating directional selection by predation strategies emergent in the Mississippian.

The reversal in camerate defensive trends, and more specifically complex camerate fortunes after Hangenberg, is probably coincident with increased predator lethality and efficiency, because predation rates were consistent (6, 12). During the Devonian, the primary method of predation was shearing, as inferred from placoderm morphology as well as recorded damage (6). In contrast, the Mississippian vertebrate radiation was defined by crushing predators. Crushers represent 57% (40 of 71) of all chondrichthyans by the end of the Tournaisian vs. 21% (8 of 37) of the smaller Famennian shark fauna (11).

Camerates with large calyces and numerous plates had success throughout the Devonian and the Tournaisian recovery interval. However, these complex morphologies were possibly much more susceptible to crushing attacks compared with simplified forms. The high numbers of sutures in complex calyces potentially increased the chances of structural failure when large areas of pressure were applied. Alternatively, crinoids with simple calyces might have been r-strategists capable of overcoming predator-induced losses via rapid growth and reproduction (36). This would confer an advantage over complex taxa in a time of increasing predation pressure (36).

Unfortunately, movement of complex camerate lineages toward the new, simplified, optimum would have first required the loss of Devonian-era defensive traits, such as thickened plates and spines (6, 14). These defenses may have had some marginal value against the newly evolving crushers or remaining shearing predators in the Mississippian. As noted above, the diversity of complex-armored camerates actually increased during the Tournaisian, when predator numbers were low. Thus, individual selection for maximal armor (numerous spines and thick plates) would act at cross-purposes to group selection for simplified armor, leading to the loss of entire lineages without significant morphological change among victims or survivors (20). In the proposed scenario of camerate decline, Devonian-era camerate defenses represent "legacy adaptations"—once beneficial but subsequently obsolete traits that prevented movement toward a new optimum.

The above explanation for camerate failure fits the data. To further test this hypothesis, we are planning more detailed studies of predator-driven trends using biomechanical models, lineage tracking, and other paleoecological methods. Our results suggest a persistent and pervasive trophic relationship between durophagous fishes and camerate crinoids during the Paleozoic, with major effects on prey diversity. Losses among Devonian fishes during the Hangenberg event seem to have indirectly led to losses among their coevolved prey by permitting the rise of more efficient predators. This knock-on effect might be common in the aftermath of trophically selective events. Finally, the trends observed here indicate that microecological phenomena, such as trophic cascades, might operate at higher levels with long-term macroevolutionary impacts.

Materials and Methods

We compiled genera-level occurrence data for Devonian-Mississippian crinoid clades and durophagous vertebrates from datasets assembled by Sallan and Coates (11), Ausich and Kammer (30, 32–34), Kammer and Ausich (12, 31), Cook (35), and Waters and Webster (13). Gnathostome and crinoid data were revised through surveys of the literature and museum collections, as well as extensive revision of published systematics, and description of new faunas in the case of the latter. Potential Devonian durophages (MPMR predators) included various placoderms (ptyctodonts and various arthrodires) and lungfish; whereas potential Mississippian durophages (postextinction replacements) included chondrichthyans (holocephalans, elasmobranchs, and other clades) and actinopterygians (amphicentrids and other genera). Members of all these groups fed at least intermittently on crinoids during the Devonian and/or Mississippian, on the basis of gut contents, coprolites, recorded damage to other benthic invertebrates, and predation on echinoderms by modern analogs among holocephalans, sharks, and teleosts (17, 22, 23). Genera were binned by stages with dates based on Gradstein et al. (37), resulting in 666 crinoid occurrences and 354 durophagous fish occurrences (*SI Appendix, Supporting Methods and Discussion* and Table S1).

Crinoid and durophagous gnathostome genera-level occurrences from the Mississippian of North America and the British Isles were assigned to one of 11 nearly equivalent time bins used by Ausich and Kammer (30, 32–34) and Kammer and Ausich (31) (*SI Appendix, Supporting Methods and Discussion* and Table S2). This was done to examine more detailed patterns of diversification. Range-through methods of taxon compilation, combining occurrences from both North America and the British Isles, were used to counteract the effects of sampling bias and outcrop size limits in either area. This resulted in 671 camerate and advanced cladid occurrences and 416 vertebrate occurrences (*SI Appendix, Supporting Methods and Discussion* and Table S2). Serpukhovian 2 was excluded from results presented in the text because of poor sampling of crinoids, as well as vertebrates outside the Lagerstätten of Bear Gulch, Montana (11). This phenomenon reflects the relative lack of preserved marine rocks from the upper Serpukhovian.

Mississippian diversity curves for durophagous fish, camerates, and advanced cladids were subjected to runs tests on PAST 2.02 (38). Runs tests are used to determine whether the observed pattern of diversification differs significantly from a random walk, through comparison of the number of observed runs to the number of potential runs (38). PAST requires that any time series have more than 10 data points. Unfortunately, this excluded analysis of the overall Givetian–Serpukhovian dataset or separate analysis of Tournaisian and post-Tournaisian patterns for camerates. For series containing fewer than 20 points, PAST runs a Monte Carlo procedure to produce 10,000 replicates.

Significance of correlation (*P*) for all time series was based on a two-tailed *t* test (α ≤ 0.05) (*SI Appendix, Supporting Methods and Discussion* and Tables S3 and S4). This was done for both the raw data and after first differencing, a method of removing the effects of autocorrelation by only comparing changes between bins. As expected because of reduction in power, FD results were more conservative than raw counts (4). The results of all analyses are presented in *SI Appendix,* Tables S3 and S4.

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