

Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution

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It has been argued that increases in predation over geological time should result in increases in defensive adaptations in prey taxa. Recent *in situ* and laboratory observations indicate that cidaroid sea urchins feed on live stalked crinoids, leaving distinct bite marks on their skeletal elements. Similar bite marks on fossil crinoids from Poland strongly suggest that these animals have been subject to echinoid predation since the Triassic. Following their near-demise during the end-Permian extinction, crinoids underwent a major evolutionary radiation during the Middle–Late Triassic that produced distinct morphological and behavioral novelties, particularly motile taxa that contrasted strongly with the predominantly sessile Paleozoic crinoid faunas. We suggest that the appearance and subsequent evolutionary success of motile crinoids were related to benthic predation by post-Paleozoic echinoids with their stronger and more active feeding apparatus and that, in the case of crinoids, the predation-driven Mesozoic marine revolution started earlier than in other groups, perhaps soon after the end-Permian extinction.

macroecology | macroevolution | predation | escalation | cidaroids

Predator–prey interactions may represent a significant driving force of evolutionary change (1–4), but predation and its consequences are often difficult to assess in Recent communities and even more so in the fossil record. Data on fossil and extant crinoids, commonly known as sea lilies and feather stars (Echinodermata), indicate that they suffer from predation by fishes, and numerous evolutionary trends have been ascribed to such interactions (5–15). Among these are (i) crawling and swimming abilities in comatulids (6), (ii) choice of semicryptic habits and nocturnal–diurnal behavior among comatulids (6), (iii) increasing plate thickness and spinosity among Paleozoic crinoids (9), (iv) offshore displacement of late Mesozoic/Cenozoic stalked crinoids (11), and (v) origin of autotomy (shedding) planes in the stalk and arms (13). Some of these trends have served as examples of dramatic change in marine ecosystems, such as the Mesozoic marine revolution (MMR) (2, 16) and the middle-Paleozoic marine revolution (9).

Although predation by fish has received the most attention, crinoids may be the prey of other organisms, most notably benthic invertebrates. Until recently, few data hinted at the importance of benthic predators to crinoids, including a swimming response in a comatulid when perturbed by the predatory sea star *Pycnopodia helianthoides* (17), the presence of crinoid pinnulars in the gut of the goniatid *Plinthaster dentatus* (18), and a crinoid arm observed in the claw of the crab *Oregonia gracilis* (17). Recently, submersible studies of stalked crinoids belonging to the Isocrinidae have revealed that they are prey to cidaroids, or pencil urchins. Evidence for this interaction includes (i) *in situ* observations of cidaroids among large aggregations of motile isocrinid sea lilies (*Neocrinus decorus* and *Endoxocrinus parrae*), (ii) proximity of cidaroids to several up-ended isocrinids, (iii) a cidaroid perched over the stalk of an up-ended crinoid and (iv) another on top of disarticulated crinoid remains, and (v) gut contents of cidaroids consisting of as much as 70% crinoid skeletal material (19).

To further explore the interaction between extant cidaroids and crinoids, to test for evidence of the interaction in the geologic past, and to identify its evolutionary consequences, we conducted aquarium experiments, analyzed samples of Triassic fossil crinoids, and examined the evolutionary history of crinoids and echinoids.

Results

Live individuals of the commercially available cidaroid, *Eucidaris* sp., were placed together in aquaria with live specimens and detached arms of the shallow-water comatulid crinoid, *Lamprometra palmata*, as well as with isocrinid crinoid arm and stalk segments. Although cidaroids do not specialize on crinoids, every echinoid that was presented with crinoid material consumed all or part of it, and in one instance, a live *L. palmata* was eaten entirely (Fig. 1A and Movies S1). Ingested crinoid body parts consisting of multiple skeletal elements occasionally passed through the sea urchin gut and were excreted without disarticulating, remaining as multiple-element units bound together by soft tissue. Some crinoid elements that passed through the gut were marked by scratches and circular to oval pits with dimensions matching those of the teeth of the urchin's Aristotle's lantern chewing apparatus (Fig. 1C and D). In one dissected cidaroid, a multiple-element segment of a crinoid's arm marked by such scratches and pits was recovered from the very distal part of the hindgut (Fig. 1B).

The aquaria observations document that crinoids could represent sea urchin prey and demonstrate that echinoids leave characteristic scratches and pits that might be preservable in the sedimentary record. Indeed, an analysis of sediment samples collected at sites where crinoid–cidaroid interactions have been observed via submersible (19) reveal a significant proportion of crinoid elements with such pits and scratches. Furthermore, and as indicated here, an example of such markings on Jurassic crinoids has been recently described (20).

To determine whether cidaroids interacted with crinoids during the Triassic, we looked for evidence of such bite marks on more than 2,500 fragments of crinoid stalks collected from five middle Triassic localities in Poland (Fig. S1). More than 500 columnals (approximately 20%) had characteristic scratches and pits: relatively shallow, clean cuts in the stereom of the ossicle surface, 0.1 to 1.5 mm wide and as long as 2.5 mm (Fig. 2). Pits are usually oval to circular and perpendicular to the ossicle surface. These marks occur chiefly on the exposed lateral ossicle surfaces rather than on the articular faces, suggesting that they were made while skeletal elements were still articulated. This is also consistent with numerous examples of such

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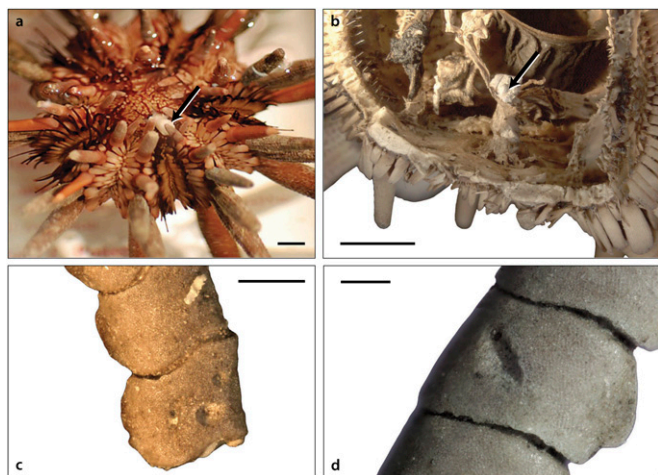


Fig. 1. In-aquaria observations of the cidaroid, *Eucidaris* sp., consuming and processing crinoid skeletal elements. (A) Oral side of *Eucidaris* sp.; arrow indicates a stalk segment of the isocrinid, *N. decorus*, held in the Aristotle lantern. (B) A dissected section of *Eucidaris* sp., aboral side down; arrow indicates a multiple-element piece of a comatulid arm at the periproct, in the distal-most part of the hindgut. (C) Multiple-element comatulid arm segment that had passed through the gut of *Eucidaris* sp. (D) Multiple-element comatulid arm segment that had passed through the gut of *Eucidaris* sp. (Scale bars: 1 mm.)

marks on well preserved pluricolumnals—isolated stalk segments consisting of more than one skeletal ossicle. Given the rapid rates of postmortem disarticulation of crinoids in natural settings (21, 22), these data suggest that the crinoid material was fresh and most probably living when the marks were made, and we treat it as evidence of predation rather than scavenging.

Although we cannot identify precisely which predators were responsible for all of the Triassic bite marks in our samples, many are similar to those we have retrieved from the guts and feces of extant cidaroids and from the sediment samples collected where cidaroid–crinoid interactions have been observed. As cidaroid spines and test fragments also occur with damaged crinoid elements at some of the Triassic localities, we conclude that crinoids were preyed upon by cidaroid echinoids that originated and diversified at this time (23, 24).

Discussion

The Triassic is considered a crucial phase of post-Paleozoic echinoderm evolution. Following the end-Permian event, which led to their near extinction, both crinoids and echinoids rebounded rapidly in the Middle and Late Triassic. This radiation led to a substantial and well known ecological diversification for both groups (25–32). Among echinoids, the post-Paleozoic radiation resulted in dramatic changes in the lantern and the teeth, with the cidaroids evolving a stronger and more active jaw apparatus (27, 28). Among crinoids, in addition to a rapid expansion through morphospace (33), major morphological and behavioral innovations led to the development of both active and passive motility (34, 35), a trait not found among Paleozoic crinoids and one that represents an effective escape strategy from benthic predators (Fig. 3). Taxa with a motile life habit included the Middle Triassic planktonic microcrinoids (roveacrinids) (31), pseudoplanktonic stalked crinoids (traumatocrinids) (34), and benthic isocrinids we now know were capable of rapid crawling (35). The primitive free-moving crinoids (paracomatulids) and pseudoplanktonic pentacrinids also likely originated in the early Late Triassic (37, 31). Similarly, although echinoid diversity apparently remained low through the Early Triassic, early cidaroids were widespread in carbonate ramp settings throughout low paleolatitude areas during the entire Triassic (32). We argue that the evolution of increased motility among crinoids was stimulated by their interactions with benthic predators, as suggested by our data on echinoid–crinoid interactions.

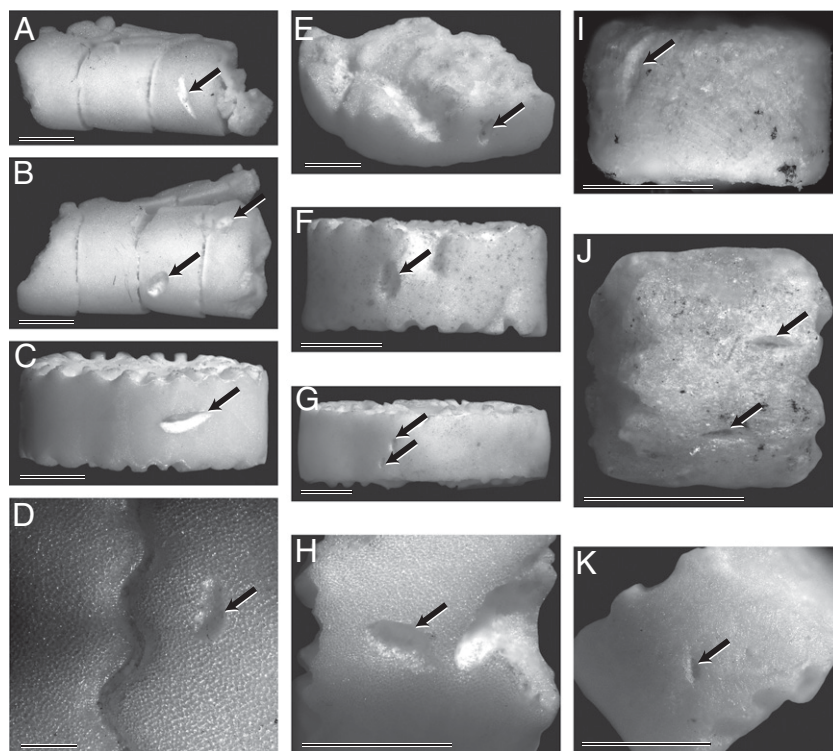


Fig. 2. Examples of bite marks (identified by arrows) on crinoid skeletal elements. Recent examples of crinoid brachials (A and B) and columnals (C and D) extracted from the gut of extant cidaroids, *Calocidaris micans* and *Histocidaris nuttingi* (19). (E–H) Recent columnals extracted from sediment samples collected by submersible at the site where crinoids and cidaroids were observed to interact (19). (I–K) Middle Triassic dadocrinid columnals collected in the Holy Cross Mountains, Central Poland. (Scale bars: 1 mm.)

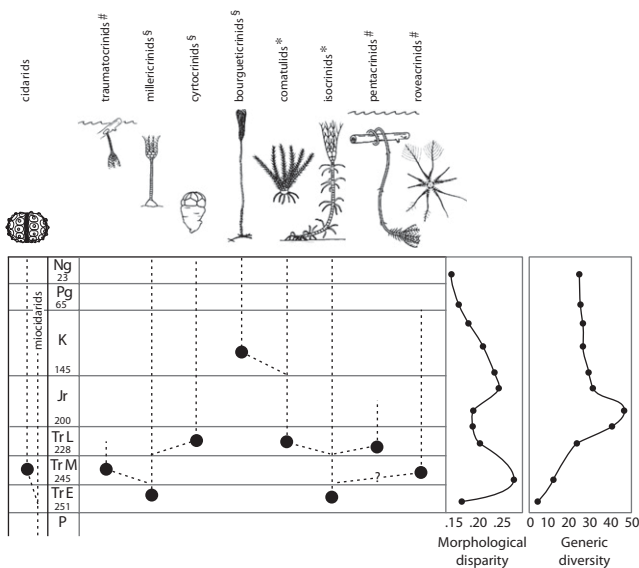


Fig. 3. Ecological, morphological (33), and generic (19, 42) diversification history of crinoids and evolutionary history of relevant echinoids during geologic periods of the post-Paleozoic. Note that ecology and morphology peak in the Triassic (Tr E, Early Triassic; Tr M, Middle Triassic; Tr L, Late Triassic), whereas generic diversity peaks in the Jurassic. Crinoid coding: §Sessile as adults; *Capable of benthic locomotion; #Nektonic, planktonic, or pseudoplanktonic. Inferred relationships modified after published reports (27, 28, 31, 36).

The MMR represented a time of fundamental change in benthic marine communities (including trends toward diversification of infauna, increased shell strength, and environmental restriction) inferred to have been caused by intensified durophagous and grazing predation (1, 2). Although considerable debate and uncertainty surrounds its onset (38, 39), the MMR is generally thought to have begun in the Jurassic and continued to accelerate in the Cretaceous (1, 2). Our data suggest that, for crinoids at least, the predation-driven MMR started in the Triassic. We argue that the major evolutionary changes characterizing many crinoid groups in the Triassic were responses to interactions with predators such as cidaroids that have generally not been considered as major players in the MMR. Of course, even with the development of motility, crinoids did not become immune from predation later in the Mesozoic. Crinoid elements from post-Triassic localities also show signs of predation (20), some characteristic of cidaroids. Durophagous fish diversified in the later Mesozoic, accompanied by the appearance of new isocrinids with arm branching patterns well suited for reducing fish-predation damage (13, 40). Moreover, the well documented pattern of offshore displacement of stalked crinoids (11) indicates that fish

might have exerted the predation pressure at this time (41). Compared with the Triassic, however, evolutionary changes in later Mesozoic crinoids were relatively minor, involving fine-tuning that predominantly led to changes in dominance (e.g., free-moving comatulids over sessile crinoids) and environmental displacement (depth restriction of stalked crinoids).

Materials and Methods

Questions pertaining to the prevalence of crinoid-echinoid interactions and the taphonomic signatures of ingested and excreted crinoid ossicles were analyzed experimentally in well established mixed-reef aquaria at Brigham Young University–Idaho. Synthetic seawater (Instant Ocean) was maintained at a relatively constant temperature of 26 °C (± 0.25 °C), salinity (specific gravity, 1.025), and pH (8.2). Live comatulid crinoids (*L. palmata*) and cidaroid echinoids (*Eucidaris* sp.) were purchased from Blue Zoo Aquatics and drip-acclimated to tank conditions for 3 h. The crinoids and echinoids were initially kept in separate tanks (125 and 65 gallons, respectively). Crinoids were not initially introduced to the *Eucidaris*-bearing tank to give the echinoids an opportunity to establish a crinoid-free diet, which consisted mostly of red and purple coralline algae that they grazed from mature live rock.

With the purpose of observing potential echinoid–crinoid interactions, two general experiment types were performed with these specimens: (i) live crinoids were transferred to the tank containing *Eucidaris*, and (ii) one or two *Eucidaris* were transferred to a 10-gallon tank and therein confined within a plastic mesh cage that included (i) a live *Lamprometra*, (ii) arms and cirri naturally autotomized or mechanically severed from live *Lamprometra*, or (iii) frozen isocrinid (*Neocrinus decorus*) stalk and arm elements collected from Jamaica via submersible. Echinoids and crinoids (or crinoid parts) were transferred to a glass-bottomed 10-gallon tank, free of substrate, to (i) increase the likelihood of echinoid–crinoid encounters, (ii) facilitate photography and video capture of the interactions, and (iii) recover bitten and excreted crinoid material. Experiments were monitored first-hand and with the aid of a time-lapse video camera (using 3–7-s intervals) from approximately 3 to 14 h. Echinoids that consumed significant amounts of crinoid material were allowed to pass some of the consumed ossicles before being preserved in alcohol. This step permitted the recovery and study of crinoid ossicles as they passed through various stages of processing by the echinoids. It also permitted direct observation, via surgical dissection, of recently consumed crinoid material in the echinoids’ digestive system.

Data on fossils were obtained from field-collected samples and museum collections (Fig. S1). The collections are housed at the Faculty of Earth Sciences, University of Silesia, Sosnowiec, Poland [catalog numbers: Geological Institute of the University of Silesia (GIUS) 7–314, GIUS 7–513, and GIUS 7–43]. Bulk samples (ca. 50 kg) of poorly lithified marly limestones were washed with hot tap water and sieved using 0.315-mm-diameter mesh. The residue was then dried at 180 °C and fossils were handpicked under a binocular microscope.

Data on the evolutionary history of post-Paleozoic echinoids and crinoids (as schematized in Fig. 3) were derived from the literature (25, 31, 36, 42).

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