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Regeneration in a stellarocrinid cladid crinoid axillary spine from the Upper Pennsylvanian Wann Formation of northern Oklahoma, USA

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Abstract

Cladid crinoid crown spines showing evidence of breakage followed by regeneration are relatively common and generally regarded as evidence of attempted predation, most likely by snipping fishes. Herein, we describe a minute spine from the Upper Pennsylvanian (Kasimovian) Wann Formation of northeastern Oklahoma, USA, that represents a stellarocrinid axillary spine. The specimen contains a single plane of breakage and subsequent regeneration, making this the first detailed description of predation-generated regeneration in an ossicle of this type, and one of few examples of regeneration in a stellarocrinid prey target. Predation-generated breakage of stellarocrinid spines is not surprising and probably reflects a general lack of attention to isolated crinoid ossicles. This occurrence of attempted predation provides further suggestive evidence that such biotic interactions likely drove the spinosity characteristic of this group.

Key words: Kasimovian, Stellarocrinidae, predation, Echinodermata, spinosity

1. Introduction

Family Stellarocrinidae comprises a relatively widespread and biostratigraphically useful cladid crinoid group (Ausich et al., 2022), with representatives consistently identified in Middle and Upper Pennsylvanian mudrock and argillaceous carbonate facies of the North American midcontinent (Holterhoff, 1996, 1997). Stellarocrinids are among the most spinose crinoids to have ever evolved, being characterized by numerous brachial spines (Fig. 1) and an array of long, radially oriented spines at the top of the anal sac (e.g., Strimple and Moore, 1971, pl. 19). The evolution of such spinosity in stellarocrinids and other cladid groups such as the pirasocrinids (see Webster, 2018) is generally interpreted as an anti-predatory strategy, directed at deterring and/or reducing the amount of critical damage inflicted by attacks by snipping fish (e.g., Meyer and Ausich, 1983; Baumiller and Gahn, 2003; Brett, 2003). Strong support for this interpretation is present in the form of abundant isolated spines that contain planes of breakage and regeneration, reflecting unsuccessful predation attempts (Baumiller and Gahn, 2003).

Despite the spinosity of stellarocrinids, there have been few published descriptions of stellarocrinid material showing evidence of regeneration, at least relative to pirasocrinids (Syverson et al., 2018; Thomka and Eddy, 2018; Thomka et al., 2022) and catacrinids (Hattin, 1958; Baumiller and Gahn, 2003). The present study focuses on a distinctive spine, identifiable as a stellarocrinid axillary plate, that shows evidence of breakage and regeneration. Such a feature in this crinoid spine type has not previously been documented explicitly and described in detail.

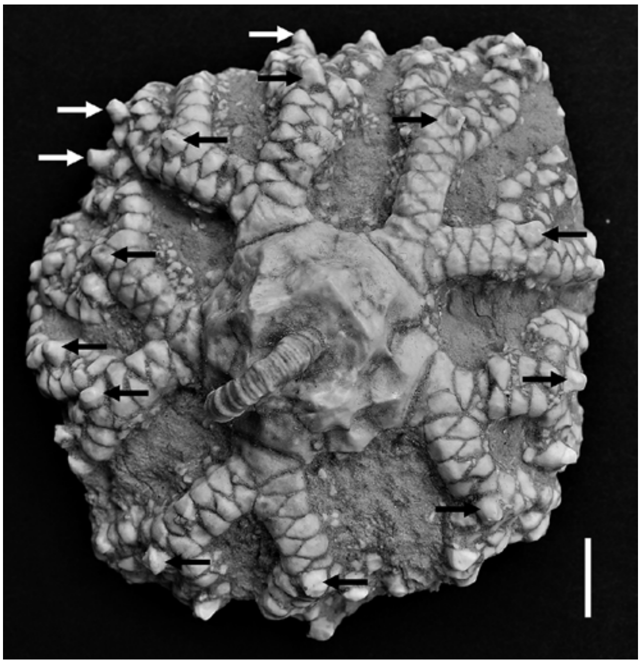

Fig. 1. Example of an Upper Pennsylvanian stellarocrinid (*Stellarocrinus virgilensis*) crown with some of the axillary spines, occurring at all arm-branching points beginning with the secundibrachials, marked by the arrows (specimen is in the paleontology teaching collection of the Center for Earth and Environmental Science, State University of New York at Plattsburgh, Plattsburgh, New York, USA). Note the distinctive shape of spine bases. The axillary spines in this particular specimen are more rounded and blunt than the specimen described in this study, due to biostratinomic abrasion, collection technique, or preparation. Scale bar = 10 mm.

2. Locality and Stratigraphy

The specimen was discovered within a relatively large collection of crinoid material consisting of isolated ossicles of multiple types, pluricolumnals and arm segments, and intact and partial cups belonging to numerous crinoid taxa. All material was surface-collected from weathered exposures of the Upper Pennsylvanian (Kasimovian; upper Missourian) Wann Formation northwest of Bartlesville, east-central Osage County, northeastern Oklahoma, USA (N36.7546°, W96.0017°). At this locality, the Wann Formation comprises crinoid-rich silty mudstone to argillaceous limestone facies deposited in an open marine, distal shelf setting (Holterhoff, 1997). Partial cups and isolated ossicles attributable to stellarocrinids are present, but are not identifiable to genus.

3. Description of Specimen

The specimen, registered as CMC IP 100001 (Cincinnati Museum Center, Cincinnati, Ohio, USA), is a minute spine, being approximately 8.0 mm in maximum length and 1.25 mm in maximum width (Fig. 2A). It is prominently tapered, terminating in a relatively sharp point (Fig. 2B), indicating that regeneration into a fully functional spine had occurred (Gahn and Baumiller, 2010). A series of striations running parallel to the long axis of the spine is present on the exterior of the specimen (Fig. 2A), a feature not observed by the authors on other spines from the Wann Formation. There is a prominent articular region at the base of the spine (Fig. 2A) that is different from equivalent portions of other spine types: at least compared to pirasocrinid spines, it lacks the adoral groove and well-developed facetal area characteristic of primibrachial spines (see, e.g., Thomka and Eddy, 2018, fig. 4) and also lacks the spatulate, polygonal spine base characteristic of anal sac summit spines (see, e.g., Thomka et al., 2022, figs. 2–3). The articular structure consists of four short, prong-like extensions separated by slightly concave areas.

The base of the spine is distinctively triangular in cross-section, representing the diagnostic feature that permits identification as a stellarocrinid axillary spine (Fig. 1). These spines are present at points of bifurcation along stellarocrinid arms, beginning at the secundibrachial and persisting at each subsequent branch point, resulting in the distinctively wide spacing between stellarocrinid arms (Strimple and Moore, 1971;

Fig. 1). There is little variation in the size of axillary spines along an arm, and the ontogenetic state of the associated individual is unknown, so it is unclear where, precisely, the spine was located on the arm. The axillary spine cannot be identified to low taxonomic levels, but its length most closely fits with *Stellarocrinus virgilensis* (Strimple, 1951; Strimple and Moore, 1971), which is known from Upper Pennsylvanian strata of the region (e.g., Strimple, 1980).

At roughly 75% of the distance along the spine as measured from the base, a prominent plane of breakage and regeneration is present, as evidenced by a sudden decrease in diameter across a sharp discontinuity (Fig. 2). The plane runs oblique to the long axis of the spine and is somewhat irregular (Fig. 2B). It is possible that this reflects a primary, irregular plane of breakage; however, this irregularity may alternatively reflect development of several lobate fronts where regeneration was occurring more rapidly than in surrounding areas (Thomka and Smith, 2019). This feature represents a single episode of breakage, presumably an unsuccessful predation attempt, followed by regeneration.

As discussed above, the morphology of this spine is clearly distinct from the well-studied spines known from other parts of spinose crinoid skeletons. The dimensions and unusual triangular base indicate that this represents distinctive spinose plates that are found at branch points (axillaries) along the arms of stellarocrinid crinoids (Fig. 1). Although located on the arms, there is no adoral groove near the articular area. Where, precisely, the spine was located along the ray is not possible to discern.

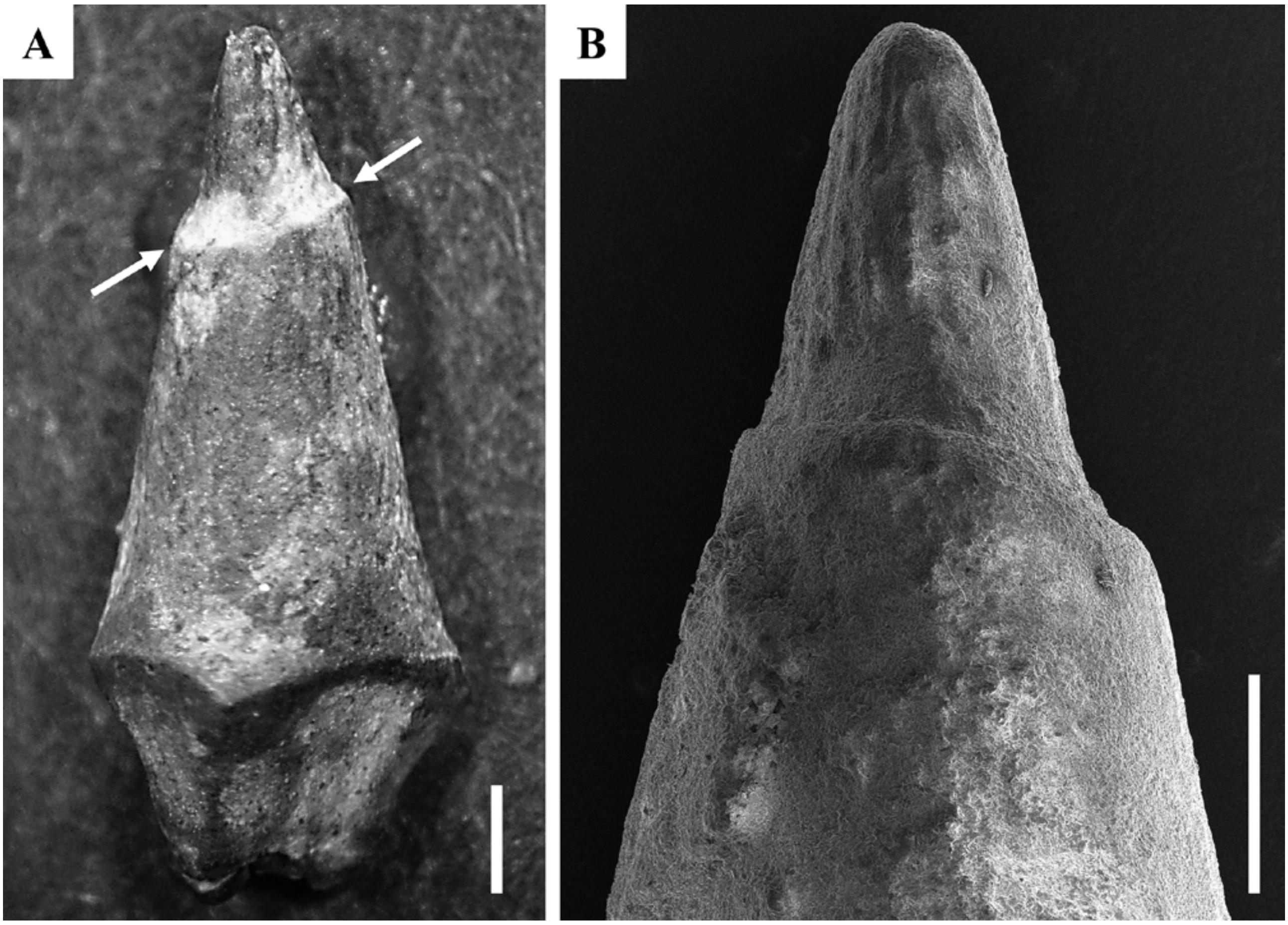

Fig. 2. A, Stellarocrinid axillary spine from the Upper Pennsylvanian Wann Formation of northeastern Oklahoma, USA (CMC IP 100001), with one plane of breakage and regeneration (marked by arrows). Regeneration, probably reflecting attempted predation, has not previously been documented in this spine type. Scale bar = 1 mm. **B,** Scanning electron photomicrograph of the axillary spine tip. Note that this image shows the opposite side of the spine from that shown in panel A. Scale bar = 0.25 mm.

4. Discussion

Regeneration of cladid spines is a relatively common phenomenon (e.g., Baumiller and Gahn, 2003; Syverson et al., 2018; Thomka and Eddy, 2018); however, all previously published descriptions dealt with primibrachial and tegmen-summit spines. The specimen described herein represents a third crinoid spine type that was broken and began regeneration during the lifespan of an individual. The position of all of these spine types on the elevated crown makes collision with the ground a highly unlikely cause for breakage, with attempted predation a much more likely mechanism. Fishes are generally regarded as the most likely predators (e.g., Brett and Walker, 2002; Baumiller and Gahn, 2003; Brett, 2003; Thomka et al., 2022), and the extreme spinosity characteristic of stellarocrinids is generally taken as evidence for frequent targeting of these crinoids by fish predators. There is no reason for this interpretation to be called into question based on the specimen described here; rather, the breakage of an arm spine may reflect damage induced by an attempt to reach the anal sac, which contained the nutrient-rich gonadic tissues, and was held enclosed within the arms (Lane, 1984).

In summary, a minute spine belonging to an undetermined stellarocrinid cladid crinoid from the Upper Pennsylvanian of midcontinental North America is reported to show evidence for regeneration following breakage. This spine faced outward at an axillary at some point along an arm. Breakage is interpreted as the result of a predatory attack, most likely by a fish, and such a feature has not previously been reported in this type of spine. Predation-generated damage to this portion of the skeleton lends support to the hypothesis that these crinoids were frequently targeted by predators—as also suggested by the extreme overall spinosity characteristic of this crinoid family.

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