

CRINOID ANAL SAC SPINES WITH MULTIPLE PLANES OF REGENERATION: PREDATION-GENERATED FEATURES IN THE UPPER PENNSYLVANIAN OF EASTERN OHIO, USA

BY

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Abstract— Primibrachial spines of pirasocrinid cladid crinoids that contain two discrete regeneration planes were recently described from the Upper Pennsylvanian Ames Member of the Glenshaw Formation in eastern Ohio, USA. This occurrence constitutes the first report of isolated crinoid ossicles showing evidence for repeated breakage and regeneration, most likely reflecting multiple predation attempts throughout the lifespan of single crinoid individuals. Herein we report specimens of pirasocrinid anal sac spines bearing multiple regeneration planes from the same stratigraphic interval as the previously described brachial spines. These specimens represent the first documentation of tegmen spines that were broken and began regeneration multiple times during the lifetime of an individual. The spines with multiple regeneration planes occur in an assemblage of spines that has the highest regeneration frequency of the entire Paleozoic, suggesting that pirasocrinid crinoids in eastern Ohio during deposition of the Ames Member were subjected to anomalously high (attempted) predation intensities. Additional examples of similar specimens are needed to generate an explanatory model for the unusual frequency of breakage and regeneration, but relationships between the morphology of pirasocrinid crowns and interactions with associated non-predatory organisms may be the most important factor in explaining the high regeneration frequency of crinoid spines belonging to this group during the Pennsylvanian.

INTRODUCTION

Isolated crinoid ossicles showing evidence for regeneration following breakage, generally interpreted as evidence of attempted predation (Baumiller and Gahn, 2003), remain relatively under-studied in spite of their near ubiquity in upper Paleozoic crinoid-rich units in the North American

midcontinent (Syverson et al., 2018; Thomka and Eddy, 2018). Although there are numerous challenges to understanding and/or quantifying predator-prey relationships using exclusively disarticulated crinoid remains, exceptional specimens are nevertheless useful in identifying paleoecological phenomena that were previously unrecognized and providing guiding questions for future studies.

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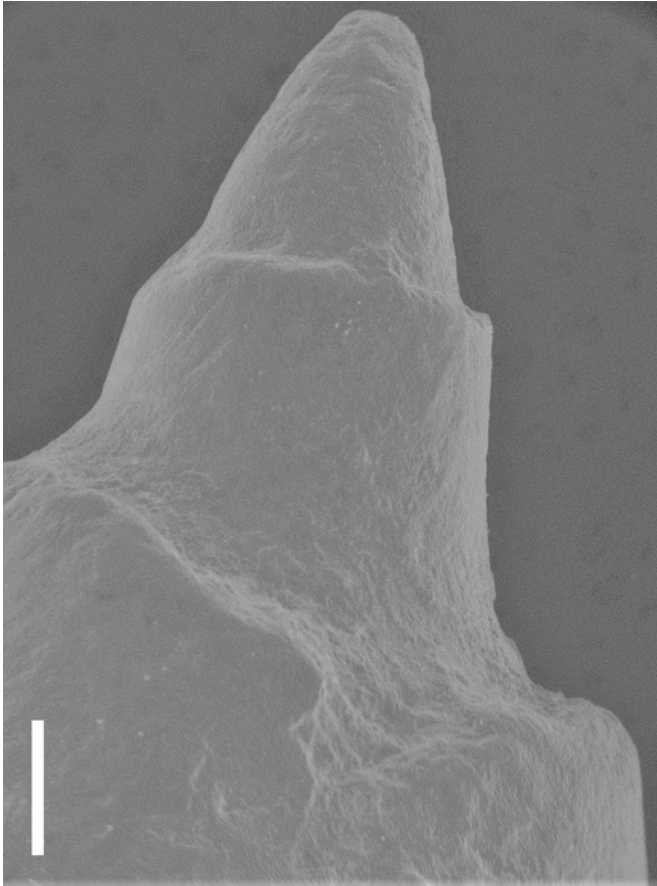


FIGURE 1 — ESEM photomicrograph of a pirasocrinid primibrachial spine with two prominent surfaces marking planes of breakage and subsequent regeneration (CMNH 9279). Thomka and Eddy (2018) reported this specimen, along with several others, from the Ames Member of the Glenshaw Formation of eastern Ohio, USA (this particular spine was depicted in Thomka and Eddy, 2018: fig. 4a). Scale bar = 1 mm.

Thomka and Eddy (2018) recently described informative primibrachial spines attributable to pirasocrinid cladid crinoids from the Upper Pennsylvanian Ames Member of the Glenshaw Formation of eastern Ohio, USA. These brachial spines were noteworthy because each specimen (five total) contained two planes of breakage and regeneration (Fig. 1), a feature not previously documented in isolated crinoid ossicles. These specimens provide unambiguous evidence that ossicles belonging to certain pirasocrinids were subjected to repeated breakage followed by partial regeneration during the lifespan of the individual. This suggests an atypically high frequency of attempted predation on pirasocrinid crinoids in the area, an interpretation that is further supported by an overall proportion of spines with evidence for regeneration that is substantially higher than that generally documented in Paleozoic spine assemblages (Syverson et al., 2018). Whereas spine regeneration frequencies typically fall within the range of 5–15% in the Paleozoic (Syverson et al., 2018), the Ames

Member assemblage is characterized by an overall spine regeneration value of approximately 35% (Thomka and Eddy, 2018).

After publication of the study on Ames Member crinoid spine regeneration by Thomka and Eddy (2018), additional specimens of direct relevance have been discovered from the same stratigraphic interval. Therefore, the present report represents a supplement to Thomka and Eddy (2018), focusing on significant crinoid spines not previously described. This addendum is necessary because the initial study dealt exclusively with pirasocrinid primibrachial spines, whereas the material considered here consists of anal sac spines (Figs. 2–3). Although evidence for breakage and regeneration of pirasocrinid anal sac spines along single planes has been documented previously (e.g., Burke, 1973; Syverson et al., 2018), the presence of multiple regeneration planes on ossicles of this type has not hitherto been described. Hence, the objectives of this paper are to describe the occurrence of pirasocrinid anal sac spines with evidence of repeated regeneration and to discuss these specimens in the context of predator-prey dynamics during the late Paleozoic.

INSTITUTIONAL ABBREVIATIONS

CMNH — Cleveland Museum of Natural History, Cleveland, Ohio, USA.

MATERIALS AND METHODS

Studied material is deposited in the invertebrate paleontology collections of the Cleveland Museum of Natural History under specimen number CMNH 9211. This is a specimen lot of more than 100 isolated pirasocrinid crinoid ossicles, including anal sac spines, primibrachial spines, basal plates, and radial plates. Although some of the radials appear to belong to the genus *Plaxocrinus* Moore and Plummer 1937, the anal sac spines described here may have come from a different taxon or taxa as isolated pirasocrinid anal sac spines cannot be confidently identified to a genus (Lewis, 1974).

Specimens were collected from the Upper Pennsylvanian (Kasimovian; Missourian to Virgilian) Ames Member of the Glenshaw Formation, which is included within the Conemaugh Group. This interval comprises one of the “marine zones” within a succession of cyclothems, representing the maximum transgressive phase of the Conemaugh Group and development of shallow, open marine environments throughout eastern Ohio. The specific collection locality is a roadcut exposure along the westbound lane of OH-40 (E. Pike Rd.) in between Cambridge and Old Washington, Guernsey County, east-central Ohio, USA (N 40.03889°, W 81.39167°). The Ames Member consists of a bioturbated, fossiliferous wackestone at this locality and nearby exposures (Thomka and Eddy, 2018). An environment characterized by normal marine salinity and relatively slow sedimentation is inferred.

The collection of separated crinoid plates (CMNH 9211) was sorted by ossicle type, with anal sac spines comprising approximately one third of the specimens. All anal sac spines

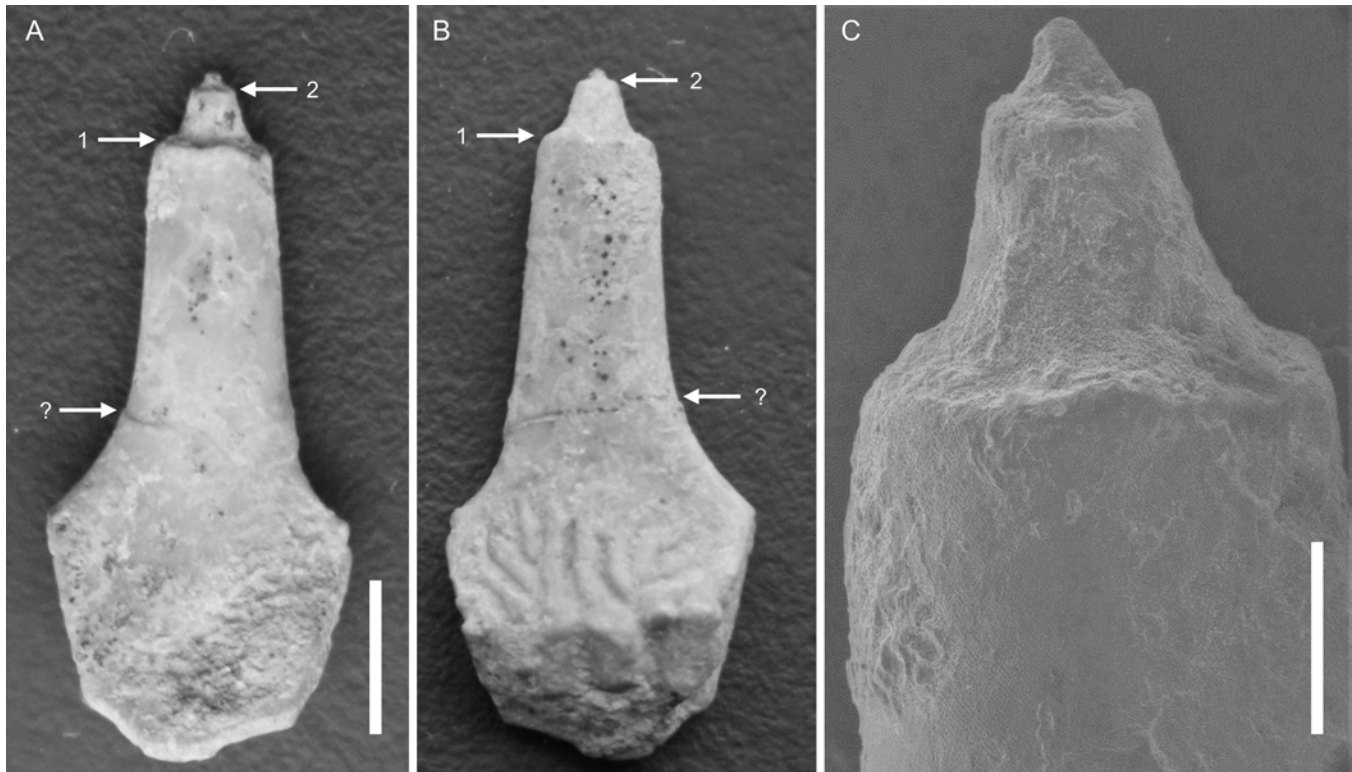


FIGURE 2 — Pirasocrinid anal sac spine (CMNH 9211-A) with multiple planes of breakage and regeneration. **A, B**, Upper (=ventral; A) and lower (=dorsal; B) surfaces of the entire spine with planes of regeneration marked by numbered arrows. The arrow with the question mark shows a planar feature that is most likely a fracture and not a plane of regeneration. Scale bar for both panels (shown in A) = 5 mm. **C**, ESEM photomicrograph of the distal portion of the spine showing the sharpness of the planes of breakage and regeneration. Scale bar = 1 mm.

were closely inspected for regeneration planes, and those with multiple regeneration planes were photographed using an environmental scanning electron microscope (ESEM). The ESEM permitted up to 1000x magnification, but most useful images that clearly show the regeneration planes are from 90–200x magnification; greater magnification revealed the details of surprisingly well-preserved stereomic microstructure (Thomka and Smith, 2019). Specimens required no coating for ESEM imaging to be employed.

SPECIMEN DESCRIPTIONS

Two isolated anal sac spines in CMNH 9211 display evidence of repeated regeneration in the form of two distinct planes of breakage present on each specimen (Figs. 2–3). Planes of breakage are marked by sharp discontinuities along the long axis of the spine shaft, with regenerated portions represented by sudden decreases in the diameter of spines. The regenerated portions are grown in the same direction as the unbroken parts of the spine (i.e., there has been no noticeable deflection in growth direction). Tips are relatively sharp in the distalmost portions of regenerated spines (Fig. 2C; see also Fig. 1), indicating that regeneration into a functional spine

had occurred or was near completion at the time of separation from the rest of the crinoid crown (Gahn and Baumiller, 2010). There is no evidence that breakage occurred preferentially along cleavage planes in any of the specimens.

The specimen in Figure 2 (herein designated CMNH 9211-A) is slightly more than 18 mm in maximum length and is light gray in color. Two prominent planes of breakage and regeneration are present, both being relatively close to the spine tip (Figs. 2A–B). The more proximal plane is approximately 2 mm from the spine tip and is oriented perpendicular to the long axis of the spine. It is slightly irregular, with a somewhat jagged appearance, particularly on the dorsal side (Figs. 2B–C). The more distal plane is approximately 0.25 mm from the spine tip. It is oriented perpendicular to the long axis of the spine and is regular (Fig. 2C). The difference in the regularity of the regeneration planes on this spine may reflect the primary geometry of the breakage plane (i.e., the earlier event broke the spine along a more irregular plane than the later event). Alternatively, it may reflect the greater amount of regeneration associated with the earlier plane, along which spine diameter may have increased during regrowth heterogeneously rather than uniformly (see Thomka and Smith, 2019). Interestingly, there is a third planar feature at the very base of the spine shaft

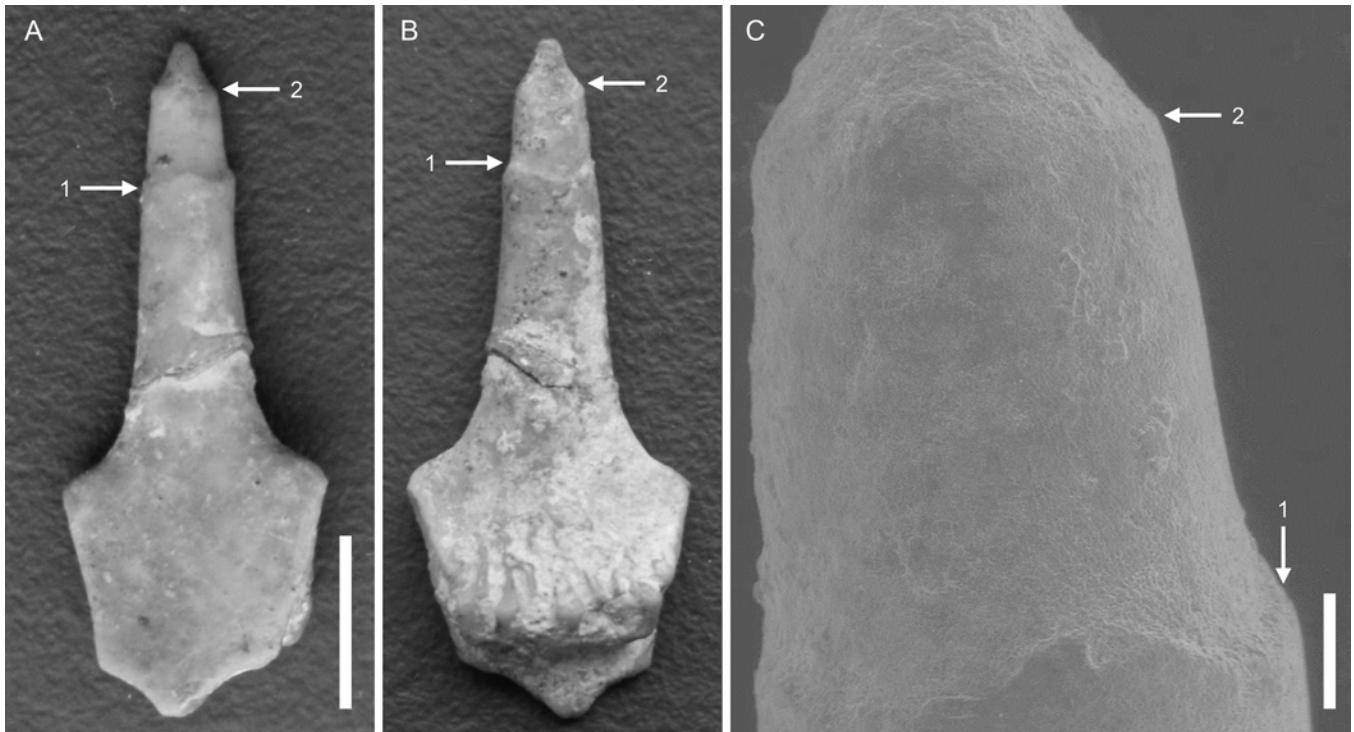


FIGURE 3 — Pirasocrinid anal sac spine (CMNH 9211-B) with multiple planes of breakage and regeneration. **A, B**, Upper (=ventral; A) and lower (=dorsal; B) surfaces of the entire spine with planes of regeneration marked by numbered arrows. The discontinuity running obliquely through the base of the spine is a fracture and not a third plane of regeneration. Scale bar for both panels (shown in A) = 5 mm. **C**, ESEM photomicrograph of the medial to distal portion of the spine with planes of regeneration marked by numbered arrows. Note the subtlety of the plane labeled 1, indicating that the spine had regenerated to nearly its entire pre-breakage diameter. Scale bar = 0.5 mm.

(the neck *sensu* Lewis, 1974) that is relatively subtle (marked by the question mark on Figs. 2A–B). Although there appears to be a small offset in spine diameter across this surface (Fig. 2A), this plane does not appear to be a regeneration plane and is more likely a fracture (Fig. 2B) that was produced after death of the crinoid.

The specimen in Figure 3 (herein designated CMNH 9211-B) is slightly less than 20 mm in maximum length and is purplish-brown in color. Two planes of regeneration are present, one being relatively subtle and the other being more prominent. Both planes are oriented roughly perpendicular to the long axis of the spine. The more proximal plane is located approximately 4 mm from the spine tip and is the subtler plane (Figs. 2A–B). As with the spine described above, this earlier plane of regeneration is somewhat irregular and jagged (Figs. 2A–B) and, as above, it is unclear whether this is the result of an irregular plane of breakage or heterogeneity along the re-growth margin. There is little difference in spine diameter across this plane (in contrast to both planes in the other specimen; Fig. 2), suggesting that the spine had nearly returned to its pre-breakage diameter. The more distal plane of regeneration is located 1 mm from the spine tip and is characterized by a more dramatic change in spine diameter (Fig. 3C). However, the most proximal portion of the spine

regenerated from this plane appears somewhat tapered toward the spine tip rather than occurring as an immediate shift to a lower-diameter section (Fig. 3C).

In all cases, the more proximal regenerated portion is characterized by a larger diameter than the more distal regenerated portion (Figs. 2–3). This indicates that the regenerating portion of a broken spine had not yet reached its original (pre-breakage) diameter before a distal portion of the regenerating spine was, itself, broken. It is therefore indisputable that (at least) two distinct events occurred to the ossicles described here that resulted in intraplate breakage without resulting in death of the crinoid or diminished regenerative capacity of the spine.

DISCUSSION

The features described here indicate that pirasocrinid anal sac spines were broken and (at least partially) regenerated more than once during the lifespan of the crinoid from which they came. Predatory attacks, most likely by fishes, are widely accepted as the most likely cause of this style of damage to late Paleozoic crinoids, at least when occurring in association with single regeneration planes (Burke, 1973; Meyer and Ausich, 1983; Brett and Walker, 2002; Baumiller and Gahn, 2003;

Brett, 2003; Syverson et al., 2018; Thomka and Eddy, 2018), although cephalopods cannot be definitively ruled out as the cause of breakage. Several potentially durophagous fishes that could have served as the predators responsible for the broken spines are known from the Ames Member, so fish are herein considered as the most likely candidates. Post-breakage regeneration unambiguously demonstrates that the recorded predation attempts were non-lethal to the crinoids, with the individual surviving long enough to begin spine regrowth, but being damaged again before the regenerating portion of the spine could return to its full pre-breakage diameter.

Individual crinoid ossicles, in the form of pirasocrinid primibrachial spines, that contained multiple planes of regeneration were first described by Thomka and Eddy (2018). The occurrence of additional spines from a different part of the crinoid skeleton, described here, indicate that the phenomenon of repeatedly regenerated spines is not unique to the previously described specimens. However, to date, ossicles with multiple planes of breakage and regeneration have only been reported from pirasocrinids from the Ames Member of the Glenshaw Formation of eastern Ohio—representing the same stratigraphic unit, geographic area, and crinoid family that were initially described.

The restriction of spines with multiple regeneration planes to the Ames Member of the Glenshaw Formation in eastern Ohio is difficult to explain, as pirasocrinids are widespread and abundant in Upper Pennsylvanian marine strata of North America (Holterhoff, 1997; Webster, 2018), and isolated pirasocrinid ossicles, including brachial and anal sac spines, are common bioclasts in many marine sedimentary deposits of this age. This may be the result of specimens from other localities simply being overlooked in existing collections. This does not appear to be a sufficient explanation by itself, however, as the relatively comprehensive study of cladid crinoid spines by Syverson et al. (2018), which evaluated hundreds of pirasocrinid spines from throughout the North American midcontinent, including collections from similar depositional environments to the Ames Member, did not yield specimens with multiple regeneration planes. Further, the high overall frequency of regeneration planes in pirasocrinid spines from the Ames Member in eastern Ohio—35% (Thomka and Eddy, 2018), which is more than double the typical frequency for Pennsylvanian crinoids (Syverson et al., 2018)—indicates that predation intensity may have truly been unusually high in this region. The state of preservation of spines from the Ames Member is not spectacular and is identical to the spines studied by Syverson et al. (2018), so taphonomy does not appear to be a factor. More information is needed to resolve this issue.

The restriction of spines with multiple regeneration planes to this single cladid family may be related to certain morphological aspects of pirasocrinids. First, pirasocrinids are among the most spinose of crinoids to have ever evolved (Lewis, 1974; Syverson et al., 2018). With numerous spines on each arm in addition to a radial array of spines atop the hypertrophied, mushroom-shaped anal sac (Lewis, 1974; Thomka and Eddy, 2018: fig. 1), a large number of spines

are present on each pirasocrinid individual. Rare or unusual features of isolated spines belonging to pirasocrinids may be more likely to be discovered simply because of the sheer number of spines that can be collected from deposits that contain a rich pirasocrinid fauna. However, as also noted above, such specimens were not identified among the Pennsylvanian cladid crinoid spine assemblages studied by Syverson et al. (2018).

Biotic interactions may play a more important role in explaining the high pirasocrinid spine breakage values. Thomka and Eddy (2018) outlined the morphological and ecological factors that relegated pirasocrinids to the category of relatively poor prey items compared to co-occurring and/or common and coeval crinoid taxa—but taxa that were nevertheless subjected to frequent predation attempts. Pirasocrinids themselves do not make sense as targets of intense predation; for example, the large size of anal sacs was attained primarily through addition of roofing plates, spines, and intercalated, spine-bearing tegmen plates rather than expansion of the interior cavity of the tegmen. The hypertrophied anal sac may have assisted with respiration but did not appear to house an unusually voluminous or nutritious gonadic payload (Lewis, 1974; Lane, 1984). Rather, the most logical explanation for this apparent paradox is that the pirasocrinids were not the actual intended target and that associated organisms that were interacting with the pirasocrinids, specifically in the region of their crowns, were the true targets of predation (see Brett and Walker, 2002; Brett, 2003; Syverson et al., 2018; Thomka and Eddy, 2018).

It has been suggested that attacks on late Paleozoic crinoids may have involved non-lethal predation on expendable anal sacs and their contained gonads (Lane, 1984) followed by regeneration. The occurrence of repeatedly regenerated anal sac spines in these pirasocrinids, however, indicates that, at least in these cases, the anal sacs were retained through repeated predation attempts. As a corollary of the model of secondary targeting (Syverson et al., 2018; see also Brett, 2003), we suggest another variant of predatory behavior, non-lethal to the crinoids. Attacks on commensals, parasites, or organisms involved in some other form of association with the crinoids may actually have been successful without causing death of the crinoids, which may have encouraged repeated foraging on host crinoids. While these attacks were somewhat deleterious to crinoid hosts (via broken spines and perhaps other collateral damage), they could have been largely innocuous, or even beneficial to some extent if antagonistic organisms were removed without significant damage to the crinoid. Thus, the high frequency of attacks on pirasocrinids may involve their propensity to attract associated symbionts and/or epifauna.

For Devonian and Mississippian crinoids, it has been postulated that the known association of platyceratid gastropods with particular host crinoids increased the frequency of attacks on the hosts and may have driven an evolutionary response in the form of increasing spinosity through time; evidence for this hypothesis lies in the non-random association of platyceratid hosts and evolution of

spinosity (Brett, 2003; Syverson et al., 2018; Thomka and Brett, 2021). Although pirasocrinids have not yet been found in association with platyceratids in the Ames Member, three factors must be considered when evaluating the secondary targeting hypothesis in this instance. First, pirasocrinid crowns disarticulate rapidly after death, making them among the most likely of Pennsylvanian crinoid morphotypes to be discovered exclusively as isolated ossicles (Thomka et al., 2012). This would obscure the evidence for association with a platyceratid unless the attached gastropod shell managed to hold identifiable cup plates together. Second, platyceratids are known to infest Pennsylvanian stellarocrinid crinoids (e.g., Strimple and Moore, 1971: pls. 18.5, 19.4), which are similar in morphology to pirasocrinids in having spinose brachials and a spinose tegmen capped by a radiating set of anal sac spines. Hence, it is not unreasonable to infer that pirasocrinids were at least capable of serving as hosts to platyceratids, although this association has not been confirmed. Third, a preliminary assessment of evidence for biotic interactions recorded on isolated cup plates from the Ames Member showed that 50.0% of pirasocrinid ossicles (33 out of 66 specimens) had encrusters, borings/embedment structures, short slashes, and/or meandering bioerosion structures. This value was higher than that for co-occurring, moderately spinose catacrinids (33.3%, 11 out of 33 specimens) and non-spinose cromyocrinids (24.6%, 49 out of 199 specimens). An abundance of specimens bearing such features is consistent for pirasocrinids described from other Pennsylvanian localities (Pabian et al., 1997; Pabian and Rushlau, 2002). Hence, despite the absence of a definitive association with platyceratids, pirasocrinids may have been subjected to secondary targeting. Modern crinoids serve as hosts to large numbers of commensals and parasites, including annelids, arthropods, ophiuroids, and cnidarians (e.g., Meyer and Ausich, 1983; Zmarzly, 1984; Fabricius and Dale, 1993), many of which are entirely soft-bodied, lightly mineralized, or not tightly associated with the crinoid and, therefore, incapable of leaving a robust record of the interaction. It is quite probable that Paleozoic crinoids similarly harbored symbionts and faunal associates, which could have provided a ready food source for swimming predators. At present, however, this must remain a hypothesis pending evidence of such interactions.

In a larger sense, the discovery of pirasocrinid anal sac spines that were broken and at least partially regenerated more than once during the lifespan of the associated crinoid individual demonstrates that the specimens described by Thomka and Eddy (2018) were more than isolated anomalies. At least within the Ames Member and at least among pirasocrinid cladids, spines present on crinoid crowns were being broken repeatedly. Further, given the fact that at least one plane of breakage that occurred earlier in the life history of the crinoid was relatively subtle due to attainment of near-pre-breakage spine diameter, it is worthwhile to consider the number of former planes of breakage that cannot be recognized in the fossil record due to full regeneration of missing portions of the spine in areas of less frequent

non-fatal breakage. The number of episodes of breakage determined from analysis of partially regenerated Paleozoic crinoid spines must be an under-estimation, although the extent to which this influences estimates of predatory attacks on crinoids is not known and may not be significant. Careful attention to separated crinoid ossicles, which are commonly overlooked in favor of articulated material, is needed to provide additional information on the spatio-temporal and taxonomic distributions of this phenomenon and, perhaps more importantly, on the underlying cause(s) for this biotic interaction.

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LITERATURE CITED

- BAUMILLER, T. K., and F. J. GAHN. 2003. Predation on crinoids. In P. H. KELLEY, M. KOWALEWSKI, and T. A. HANSEN (eds.), *Predator-Prey Interactions in the Fossil Record*, Kluwer Academic/Plenum Publishers, New York, pp. 263–278.
- BRETT, C. E. 2003. Durophagous predation in Paleozoic marine benthic assemblages. In P. H. KELLEY, M. KOWALEWSKI, and T. A. HANSEN (eds.), *Predator-Prey Interactions in the Fossil Record*, Kluwer Academic/Plenum Publishers, New York, pp. 401–432.
- _____, and S. E. WALKER. 2002. Predators and predation in Paleozoic marine environments. In M. KOWALEWSKI and P. H. KELLEY (eds.), *The Fossil Record of Predation*. Paleontological Society Papers 8, pp. 93–118.
- BURKE, J. J. 1973. Four new pirasocrinid crinoids from the Ames Limestone, Pennsylvanian, of Brooke County, West Virginia. *Annals of the Carnegie Museum*, 44: 157–169.
- FABRICIUS, K. E., and M. B. DALE. 1993. Multispecies associations of symbionts on shallow water crinoids of the central Great Barrier Reef. *Coenoses*, 8: 41–52.
- GAHN, F. J., and T. K. BAUMILLER. 2010. Evolutionary history of regeneration in crinoids (Echinodermata). *Integrative and Comparative Biology*, 50: 514a–514m.
- HOLTERHOFF, P. F. 1997. Paleocommunity and evolutionary

- ecology of Paleozoic crinoids. In J. A. WATERS and C. G. MAPLES (eds.), *Geobiology of Echinoderms*. Paleontological Society Papers 3, pp. 69–106.
- LANE, N. G. 1984. Predation and survival among inadunate crinoids. *Paleobiology*, 10: 453–458.
- LEWIS, R. D. 1974. Studies in the inadunate crinoid family Pirasocrinidae. Unpublished M. S. thesis, University of Iowa, Iowa City, 181 pp.
- MEYER, D. L., and W. I. AUSICH. 1983. Biotic interactions among Recent and among fossil crinoids. In M. J. S. TEVESZ and P. S. MCCALL (eds.), *Biotic Interactions in Recent and Fossil Benthic Communities*, Plenum Press, New York, pp. 377–427.
- MOORE, R. C., and F. B. PLUMMER. 1937. Upper Carboniferous crinoids from the Morrow Subseries of Arkansas, Oklahoma and Texas. *Denison University Bulletin, Journal of the Scientific Laboratories*, 32: 209–303.
- PABIAN, R. K., and W. J. RUSHLAU. 2002. Taphonomic analysis and systematic descriptions of some Late Pennsylvanian and Early Permian crinoids from southeastern Nebraska, eastern Kansas, and southwestern Iowa. *Nebraska Geological Survey Papers*, 20: 1–45.
- _____, D. MOSHER, R. D. LEWIS, and P. F. HOLTERHOFF. 1997. Prey-predator, parasitic, and commensal relationships with Late Pennsylvanian crinoids and associated fauna from the Barnsdall Formation (Late Pennsylvanian, Missourian/Virgilian) of northeastern Oklahoma. *Proceedings of the Nebraska Academy of Sciences*, 107: 49.
- STRIMPLE, H. L., and R. C. MOORE. 1971. Crinoids of the LaSalle Limestone (Pennsylvanian) of Illinois. *University of Kansas Paleontological Contributions*, 55: 1–48.
- SYVERSON, V. J., C. E. BRETT, F. J. GAHN, and T. K. BAUMILLER. 2018. Spinosity, regeneration, and targeting among Paleozoic crinoids and their predators. *Paleobiology*, 44: 290–305.
- THOMKA, J. R., and C. E. BRETT. In press. Parasitism of Paleozoic crinoids and related stalked echinoderms: Paleopathology, ichnology, coevolution, and evolutionary paleoecology. In K. DE BAETS and J. W. HUNTLEY (eds), *The Evolution and Fossil Record of Parasitism: Coevolution and Paleoparasitological Techniques*, Springer, Berlin, pp. 289–316.
- _____, and D. B. EDDY. 2018. Repeated regeneration of crinoid spines in the Upper Pennsylvanian of eastern Ohio: Evidence of elevated predation intensity and significance for predator-driven evolution of crinoid morphology. *Palaaios*, 33: 508–513.
- _____, and H. K. SMITH. 2019. Stereomic microstructure of crinoid spine regeneration: Examples from the Upper Pennsylvanian of eastern Ohio. *Geological Society of America Abstracts with Programs*, 51.
- _____, D. MOSHER, R. D. LEWIS, and R. K. PABIAN. 2012. The utility of isolated crinoid ossicles and fragmentary crinoid remains in taphonomic and paleoenvironmental analysis: An example from the Upper Pennsylvanian of Oklahoma, USA. *Palaaios*, 27: 465–480.
- WEBSTER, G. D. 2018. Mississippian-Permian evolution and paleogeographic distribution of the Cromyocrinidae and Pirasocrinidae (Crinoidea, Dendrocrinida). *Swiss Journal of Palaeontology*, 137: 265–278.
- ZMARZLY, D. L. 1984. Distribution and ecology of shallow-water crinoids at Enewetak Atoll, Marshall Islands, with an annotated checklist of their symbionts. *Pacific Science*, 38: 105–122.

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