A swollen crinoid pluricolumnal from the Upper Ordovician of northern Kentucky, USA: the oldest record of an amorphous paleopathologic response in Crinoidea?

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Abstract. Swollen or otherwise malformed crinoid remains are relatively common in the Phanerozoic. However, published reports typically describe swellings associated with a discrete pit, boring, embedment structure or encruster, and, moreover, are overwhelmingly from Silurian or younger strata. Here, the rare occurrence of an amorphously swollen crinoid pluricolumnal is described from the Upper Ordovician (Katian) Grant Lake Formation of north-central Kentucky, USA. This represents one of the oldest examples of crinoid malformation potentially resulting from interaction with a parasite or epibiont, one of the oldest examples of swelling in a crinoid column, and likely represents the oldest record of amorphous swelling. The pluricolumnal is morphologically generalized, making definitive identification difficult. Potential candidates include the diplobathrid camerate *Pycnocrinus* and the large, morphologically aberrant disparid *Anomalocrinus*. Regardless, if generated by an antagonistic biotic interaction, this specimen seems to support the hypothesis that crinoids with large calyxes and relatively complex arm morphologies were preferentially utilized as hosts for parasites and commensals over crinoids with simpler morphologies in the Ordovician.

Key words: *Pycnocrinus*, *Anomalocrinus*, Echinodermata, parasitism, biotic interactions, Cincinnatian, paleopathology.

INTRODUCTION

The echinoderm skeleton is complex and dynamic. Because the skeletal plates (ossicles) that comprise echinoderm "hard parts" are precipitated as a mesodermal endoskeleton, there is potential for significant secondary modification throughout growth in response to stimuli (Raup 1966; Macurda & Meyer 1974). Further, as the echinoderm skeleton comprises a myriad of ossicles bound together in a precise and intricate arrangement by soft tissues, growth or modification of individual portions of the skeleton can occur separately from others, in contrast to the single holoperipheral growth margin of many shelled invertebrates. This permits a greater variety of skeletal modifications and increases the likelihood of discovery of modified remains even if much of the skeleton is destroyed or scattered (Donovan 1991a). Finally, the large size of echinoderm ossicles, which are precipitated as single biocrystals (e.g., Smith 1989), prevents dissolution and promotes preservation of echinoderm remains even in settings where other skeletal elements have been dissolved away (Seilacher 1973; Donovan 1991b), thereby facilitating recognition of ossicle modifications as records of paleopathologic responses.

One of the most common examples of echinoderm paleopathological skeletal modification is crinoid ossicles that are swollen or malformed by addition of secondary stereom. The earliest documentation of this phenomenon comes from Ure (1793), with descriptions continuing through the nineteenth and early twentieth centuries (Miller 1821; de Loriol 1878; Etheridge 1879; von Graff 1885; Bassler 1908). Many of these early studies incorrectly attributed the swelling to a normal growth process rather than a pathologic response. With detailed study of extant crinoids, particularly by Clark (1921), came the recognition that secondary secretion of excess stereom is commonly a response to an antagonistic relationship with an external or internal parasite.

Crinoids have a particularly strong record of preserved (or potentially preservable) biotic interactions (Meyer & Ausich 1983; Baumiller & Gahn 2004). Studies of modern crinoids have shown that biotic interactions are common in crinoid populations and involve a diverse suite of macro- and microorganisms (e.g., Fishelson 1974; Zmarzly 1984; Fabricius & Dale 1993, among many others). A diverse fauna of organisms directly associated with ancient crinoids is also inferred from the fossil record (Meyer & Ausich 1983). This interpretation is supported by the presence of encrusting

epibionts (e.g., Głuchowski 2005); parasitic or commensal organisms positioned over the anal vent or between the arms of crinoids (e.g., Bowsher 1955; Donovan 1991a; Bohatý et al. 2012); regenerated arms, columns and spines (e.g., Oji 2001; Baumiller & Gahn 2004; Gahn & Baumiller 2005); organisms contained within pits in crinoid stems (e.g., Franzén 1974; Warn 1974; Welch 1976); and predatory or parasitic borings and embedment structures (e.g., Brett 1978, 1985; Baumiller 1990). Yet, malformed (swollen) crinoid material may represent the most convincing reflection of a response to an ancient biotic interaction.

A number of studies have focused on documenting the temporal, taxonomic and paleogeographic distribution of swollen crinoid material, as well as the causes of malformations. Two of the most significant findings from these detailed studies are as follows: (1) two fundamentally different types of malformations in crinoid fossils can be recognized, namely, those associated with a discrete embedment structure, pit, boring or attachment structure, and those characterized by amorphous swelling not associated with any recognizable structures; and (2) abundant occurrences of both types of malformations are documented from Silurian and younger strata (Brett 1978), but few occurrences in Ordovician deposits are known.

Herein, we report a crinoid pluricolumnal that displays amorphous swelling. This specimen is of Late Ordovician age, making it possibly the oldest example of this specific form of paleopathology as well as one of the oldest examples of swelling in a column rather than a calyx.

LOCALITY, STRATIGRAPHY AND SEDIMENTOLOGY

The specimen was collected from a large roadcut on the east (northbound) side of Kentucky State Route 11 (KY-11) south of Flemingsburg, Fleming County, northern Kentucky (N38°21′22.849″, W83°45′32.382″; Fig. 1). This roadcut represents one of the highest in a series of exposures along KY-11 and permits construction of a fairly complete composite section of Upper Ordovician strata deposited in upper- to mid-ramp environments in the Appalachian foreland basin (Schramm 2011). The roadcut that yielded the swollen pluricolumnal exposes interbedded argillaceous, fossiliferous carbonates and dark gray, siliciclastic mudstones with fossil fragments (Fig. 2), comprising the Upper Katian (Cincinnatian: upper Maysvillian–lower Richmondian of North American terminology) Grant Lake and Bull Fork formations (Fig. 3; Weir et al. 1984). These units represent much of the C3 sequence and the lowermost portion of the C4 sequence in this part of Kentucky (Holland & Patzkowsky 2007). Recent and ongoing stratigraphic studies in this region have revealed that the upper, regressive interval of the Grant
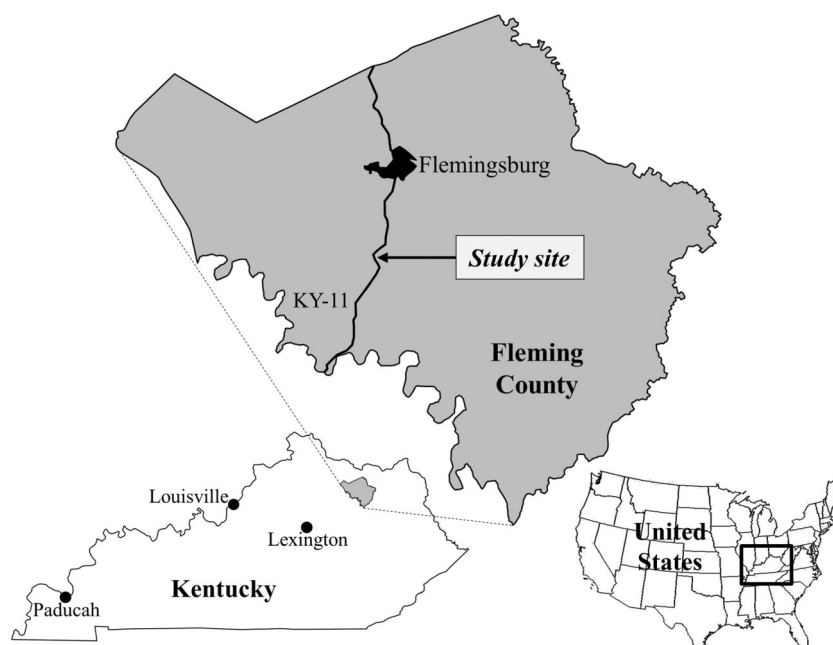

Fig. 1. Location of the study site in Fleming County, northern Kentucky, USA.
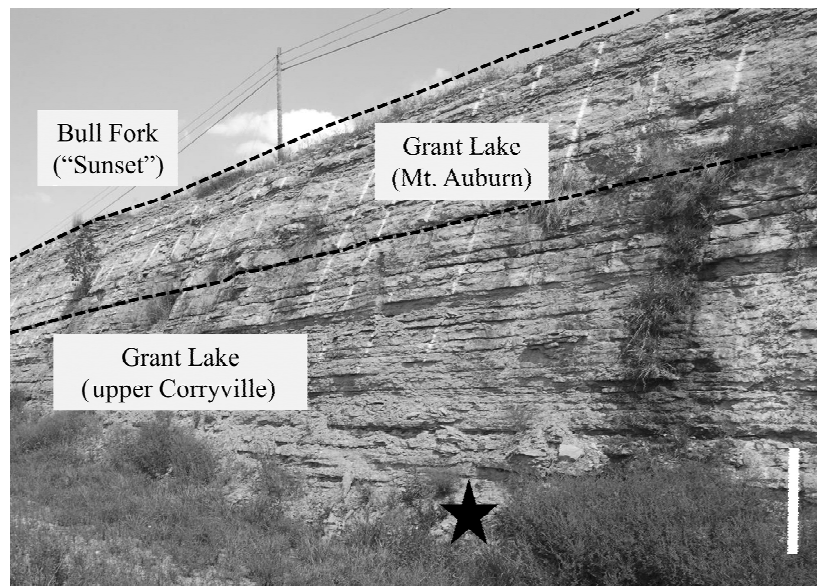
Fig. 2. Outcrop photograph of the study site, showing the upper part of the Grant Lake Formation and the lowermost, largely eroded, Bull Fork Formation. The star marks the approximate position of the talus pile from which the pluricolumnal was recovered. Scale bar = 1 m.

Lake Formation is an upramp equivalent of the upper Corryville Member of the McMillan Formation of Ohio terminology. The overlying, uppermost transgressive interval of the Grant Lake Formation correlates to the Mt. Auburn Member (McMillan Formation) and the basal Bull Fork Formation (or Sunset Member, as it is sometimes termed) corresponds to the basal Arnheim Formation (Fig. 3).

The crinoid specimen was recovered as float from a small talus pile at the base of the steep wall of the roadcut (Fig. 2). The specimen most likely came from the Corryville Member-equivalent interval of the Grant Lake Formation, as the majority of the section exposed at the site of collection belongs to this unit and because other fossils and sedimentary material in the talus pile were derived from this interval. This is worth noting because it permits a more precise source interval than the relatively unrefined Grant Lake Formation and because it allows the age of this pluricolumnal to be compared to other reports of Late Ordovician paleo-pathologically deformed crinoid material in the type-Cincinnatian region.

DESCRIPTION OF MATERIAL

The crinoid pluricolumnal (CMC IP 71254; Fig. 4) is medium brown in color, 11.4 mm long, 2.7 mm wide at the thinnest and 4.1 mm wide at the thickest point. The exact number of component columnals is impossible to determine, but at least eight are visible, all of equal height. The column is homeomorphic, with no radices or radice sockets and no obviously distinguishable nodals or internodals. It is unclear which end is proximal and which is distal. Columnals are thin, being approximately ten times as wide as tall. There is no recognizable tapering to this portion of the column. Columnals are holomeric and circular. The lumen is minute, circular and central (Fig. 4C). Neither an epifacet nor an areola is present. Columnal articulations appear to be symplectial (Fig. 4A).

One side of the specimen is damaged, reflecting post-mortem exposure and surficial biostratinomic degradation (Fig. 4B). A portion of the undamaged side of the specimen is encrusted by a thin laminar bryozoan (Fig. 4A). Although the bryozoan encrustation occurs over the most swollen portion of the pluricolumnal, it is unlikely that this interaction is responsible for the swelling. This is evidenced by (1) the occurrence of an epibiont on only one side of the column rather than around the entirety of the columnal exterior, which suggests post-mortem encrustation, (2) the observation that the bryozoan is not embedded in or enmeshed with secondary stereom, but rather overlies it (Fig. 4A) and (3) swelling that extends beyond the portion of the column that is encrusted by the bryozoan (Fig. 4A).

The swelling is amorphous and does not occur in direct proximity of a boring, embedment structure (*sensu* Brett 1985), encrusting attachment structure or organism within a cavity of any kind. The pluricolumnal is swollen uniformly with regard to the cross-sectional outline of the column (Fig. 4C), with no side more
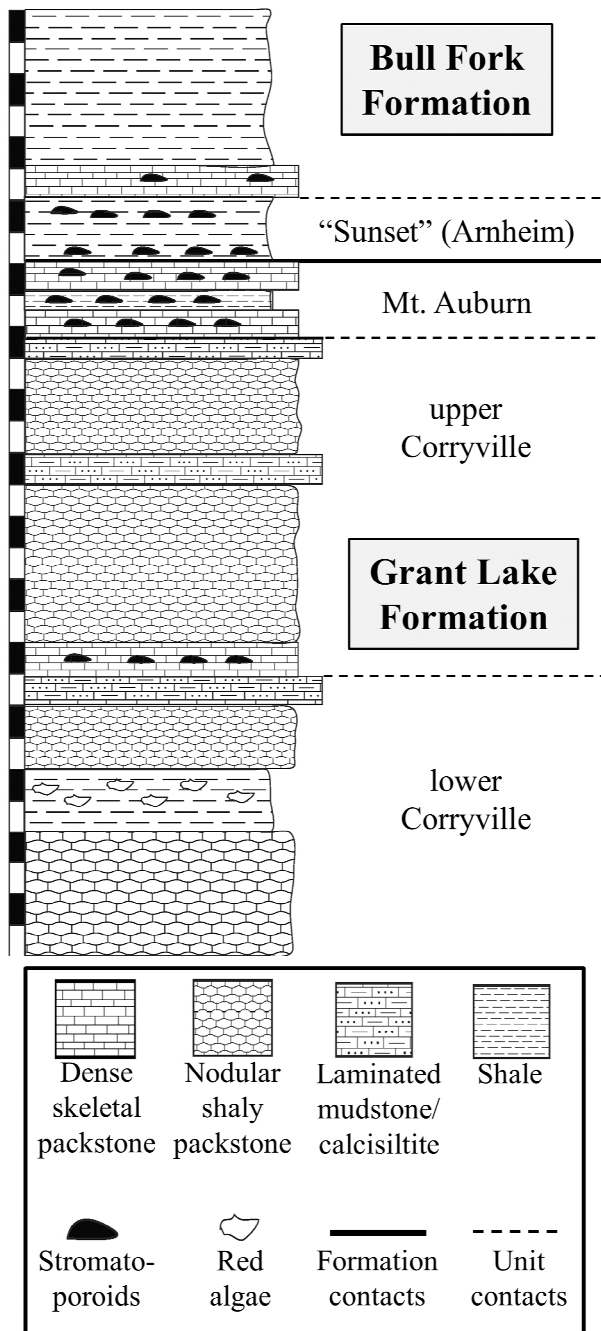
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Fig. 3. Generalized stratigraphic column for the study site. The terms within boxes indicate formation-scale lithostratigraphy for northern Kentucky and other terms represent finer stratigraphic subdivisions that correspond to the lithostratigraphic nomenclature of southern Ohio. The "Sunset Shale" is treated as the basal unit of the Bull Fork Formation, which correlates to the basal interval of the Arnheim Formation of Ohio terminology. The specimen described herein almost certainly emanated from the "upper Corryville" unit within the Grant Lake Formation. Scale bars to the left of the stratigraphic column represent meters.
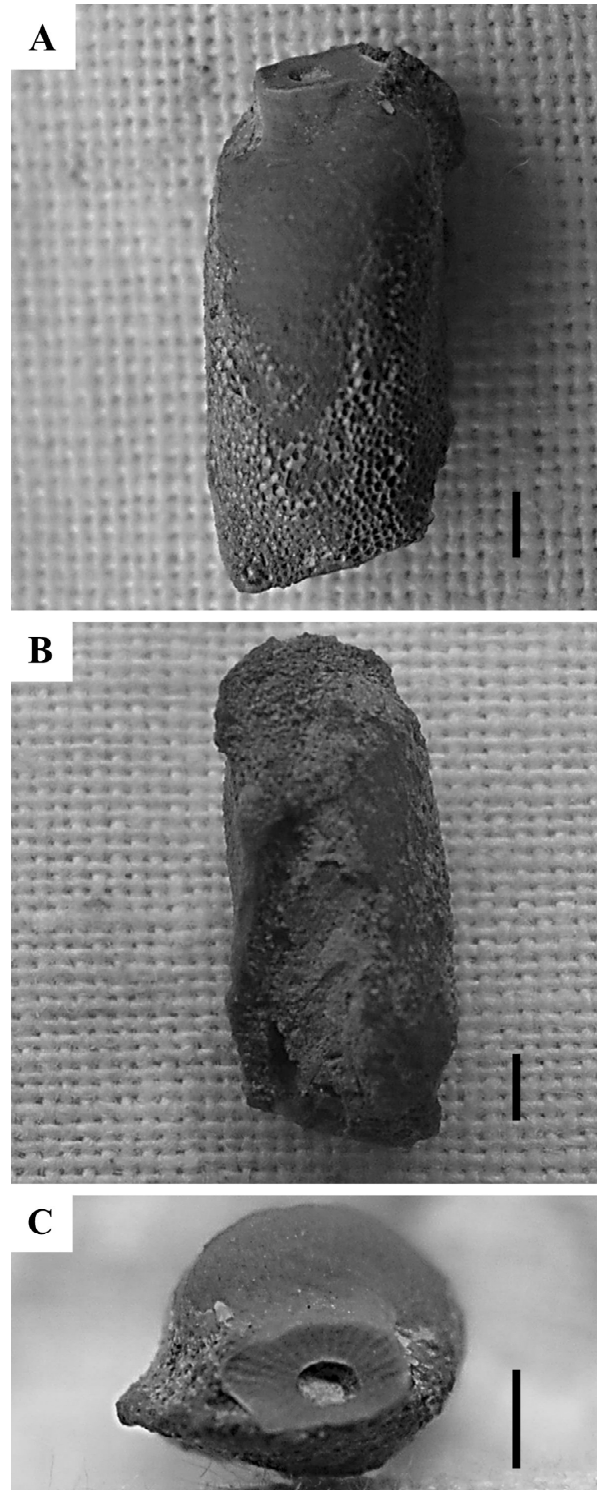

Fig. 4. Swollen crinoid pluricolumnal (CMC IP 71254) from the study site. **A**, lateral view of the specimen, showing amorphous swelling and an encrusting bryozoan; **B**, lateral view of the other side of the specimen, showing post-mortem damage; **C**, articular view of the specimen showing crenulae and small, round lumen. All scale bars = 1 mm.

severely swollen than the other, although the entire column (both swollen and unswollen portions) is somewhat compacted perpendicular to its long axis (Fig. 4C). The border between the swollen and unswollen portions of the specimen is relatively sharp, with a tapering "transition zone" slightly less than 1 mm thick (Fig. 4). The transition from swollen to unswollen portions does not correspond to a distinct suture between adjacent columnals.

DISCUSSION

Evidence for swellings induced by antagonistic biotic interactions in crinoids in the Ordovician of North America consists of hemispherical pits, sometimes irregularly malformed, representing embedment structures (*Tremichnus* of Brett 1978, 1985) and small, round, commonly swollen borings with phosphatic elements inside, representing sites of attachment (*Phosphannulus* of Warn 1974; Welch 1976; Meyer & Ausich 1983). Although the oldest *Tremichnus* are Middle Ordovician in age (Lewis 1982), these traces occur typically on calyxes and arms rather than columns and, furthermore, are not present in fossils recovered from type Cincinnatian strata. In contrast, *Phosphannulus* is relatively common in the eastern midcontinent of North America, occurs on columns, and the oldest described specimens are from the upper Maysvillian of the Cincinnati Arch region, though no details on the precise stratigraphic horizon(s) from which the material was recovered have been given (Welch 1976). Hence, the pluricolumnal studied herein is the same age as or older than the oldest paleopathological modifications to crinoid columns (at least from eastern North America). More importantly, the partial column described here is characterized by amorphous swelling not definitively associated with a discrete pit or boring. This mode of skeletal alteration is characteristic of Silurian and younger crinoid columns, but, at least to our knowledge, has not been documented in Ordovician crinoid columnal material.

Generic identification of the crinoid host is difficult given the fragmentary and poorly preserved material. Although isolated crinoid columnals can, if distinctive enough, be identified and named as morphotaxa (Moore & Jeffords 1968; Donovan 1986–1995), the morphology of the specimen studied here is too generalized to assign a columnal form-genus name. The most likely candidate for the identity of the pluricolumnal is the diplobathrid camerate *Pycnocrinus*, though this specimen is more homeomorphic than most Cincinnatian *Pycnocrinus* columns. The large disparid *Anomalocrinus* is characterized by columnals of similar dimensions in coeval sections but differs significantly in morphology; in contrast, the pluricolumnal morphology resembles that of the cladid *Merocrinus*, but this taxon does not occur in strata as young as those of the study area (Meyer et al. 2002). Definitive identification of the crinoid taxon is hindered by the relatively simple morphology of individual columns as well as the short length of the specimen. If swelling was induced by a biotic interaction, the identity of the causative organism is unknown and will likely remain so, as echinoderms are known to serve as host to a wide variety of parasites, many of which do not have an adequate fossil record (Littlewood & Donovan 2003).

It is interesting to note that both of the taxa identified as potential candidates for the producer of the swollen pluricolumnal are among the largest and most skeletally complex of Cincinnatian crinoids. Although neither genus is known for abundant skeletal malformations, *Pycnocrinus* is renowned among Cincinnatian crinoids for the high relative abundance of specimens exhibiting attached platyceratid gastropods (Ausich 1999), seemingly reflecting a commensal or parasitic relationship. Further, the genus *Glyptocrinus*, which closely resembles *Pycnocrinus*, served as an important host for encrusting commensals in the type Cincinnatian (Morris & Felton 1993). Baumiller (2003) convincingly argued that certain morphological traits of crinoids made them preferential hosts for commensal and/or parasitic organisms, with many such traits applicable to these crinoid taxa. Further, *Pycnocrinus* and *Anomalocrinus*, as well as associated large-calyx crinoids, were typically associated with some of the longest columns of the Cincinnatian (Brett et al. 2008), making these taxa capable of elevating attached or embedded organisms higher than co-occurring crinoids, offering greater protection from benthic predators and competitors and potentially exposing suspension-feeders to currents of greater velocity.

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