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Evolutionary and taphonomic implications of a new species of *Amphoracrinus* from the early Viséan of Kentucky

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Abstract.—The youngest species of *Amphoracrinus*, *A. tenax* new species, is described from the Muldraugh Member of the Borden Formation (early Viséan) of north-central Kentucky. With this new occurrence, both the oldest and youngest named species of *Amphoracrinus* are from North America. Numerous Tournaisian and Viséan crinoid faunas are documented in the United States, but only four are known to contain *Amphoracrinus*. Morphological analysis indicates that *A. tenax* is more closely aligned with species from China than with species from Western Europe or other species from North America, where *Amphoracrinus* was most diverse and abundant, which has implications for understanding paleogeographic dispersal. The holotype of *A. tenax* was partially disarticulated on the seafloor before burial, and final burial occurred early during disarticulation. The relative state of disarticulation from pinnules to columnals suggests that plates bound only with ligaments disarticulated as a function of surface area of ligaments binding an articulation.

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Introduction

An *Amphoracrinus* Austin, 1848 specimen from England was the first illustrated Paleozoic crinoid (Lister, 1673; Ausich and Kammer, 2006). *Amphoracrinus* is now known from Western Europe, the United States, and China (Tables 1 and 2). The genus had a duration of as much as 20 million years from the Famennian through the early Viséan (Mississippian). With the addition of *Amphoracrinus tenax* new species (Muldraugh Member, Borden Formation, early Viséan), 17 named species (one with a named variation) are currently assigned to this genus (Wright, 1943, 1955; Chen and Yao, 1993; Ausich and Sevastopulo, 2001; Donovan et al., 2006; Ausich and Kammer, 2006, 2008a; Webster et al., 2009) (Table 1).

Despite its relatively short temporal duration, *Amphoracrinus* spread across much of the globe in the northern tropics and subtropics, in both western and eastern Laurussia and on the Sibumasu Block, which was part of northern Gondwana during the Mississippian (present-day southern China). The most common occurrences of *Amphoracrinus* are on the Tournaisian mixed carbonate and siliciclastic ramp of southern Ireland and southwestern United Kingdom (Hook Head Formation, Ausich and Sevastopulo, 1994, 2001) and in facies associated with Tournaisian and Viséan Waulsortian buildups in Ireland, England, and Wales (Wright, 1955).

The Mississippian, recognized as the "Age of Crinoids" (Kammer and Ausich, 2006; Ausich et al., 2020a), is known for diverse and abundant crinoid occurrences, yet *Amphoracrinus* is absent from all but four North American crinoid faunas. Surprisingly, with the description of *A. tenax* n. sp. (Fig. 1), both the oldest named species, *A. viminalis* (Hall, 1863) (Meadville Shale Member, Cuyahoga Formation, early Tournaisian, Kinderhookian, late Hastarian of Ohio), and the youngest species, *A. tenax* n. sp. (Muldraugh Member, Borden Formation, early Viséan, late Osagean, Arundian of Kentucky), occur in the United States. The taphonomic implications of *A. tenax* are also discussed in this study

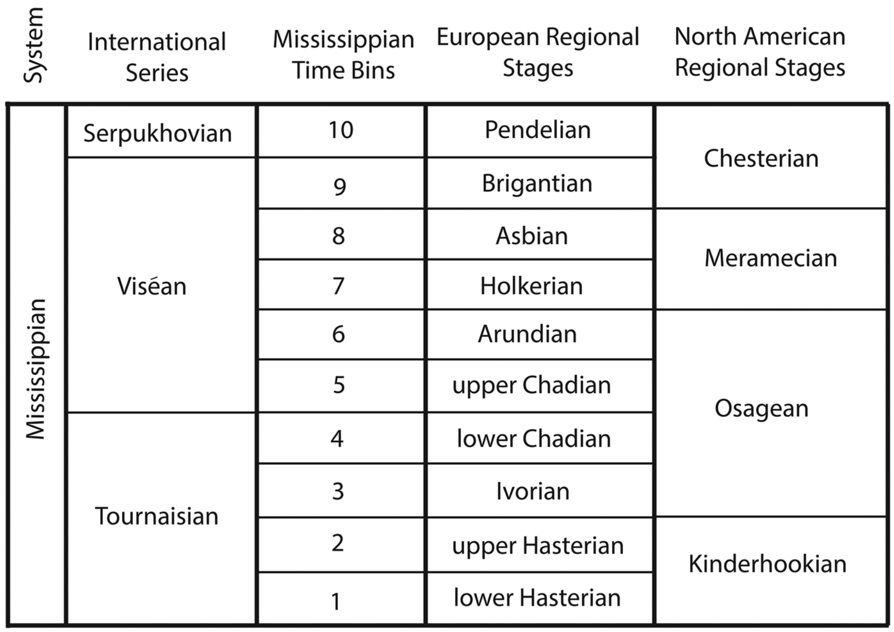
Location and stratigraphy

This new specimen was collected from the Muldraugh Member of the Borden Formation in north-central Kentucky. This location differs from the Muldraugh location (a quarry) described previously by Ausich et al. (2000) and Kammer et al. (2007). The specimen was collected from a road cut on Kentucky route 313 in Hardin County, approximately 7.3 km west of I-65 (exit 102), coordinates 37°48′23.492″N, 85°49′29.513″W (UTM 16N 591623 4184859) (Fig. 2). The road-cut stratigraphy includes (in ascending order) the New Providence Shale Member of the Borden Formation, the Muldraugh Member of the Borden Formation, and the Harrodsburg Limestone (Kepferle, 1977) that resulted from the time-transgressive, basin-filling progradation of the Borden Delta (e.g., Lane and DuBar, 1983; Richardson and Ausich, 2004). The Muldraugh Member has much lenticular bedding (Ausich et al., 2000), and this new specimen was collected from loose matrix on the surface of a

Table 1. Species of *Amphoracrinus* listed by country occurrence with appropriate international ages as well as regional stages.

Species	Country	International Series	European Regional Stages	North American Stages
A. atlas	UK	Tournaisian-Viséan	lower to upper Chadian	
A. bollandensis	UK	Tournaisian	lower to upper Chadian	
A. compressus	UK	Tournaisian	lower Chadian	
A. gilbertsoni	UK	Tournaisian-Viséan	lower to upper Chadian	
A. granulatus	UK	Tournaisian	Ivorian	
A. portlocki	UK	Tournaisian	lower Chadian	
A. rotundus	UK	Tournaisian	lower Chadian	
A. rugosus	UK	unknown		
A. turgidus	UK	Tournaisian-Viséan	lower to upper Chadian	
A. crassus	Ireland	Tournaisian	Ivorian	
A. gigas	Ireland	Tournaisian-Viséan	lower to upper Chadian	
A. gilbertsoni	Ireland	Viséan	lower to upper Chadian	
A. gilbertsoni var. *triangularis*	Ireland	Viséan	upper Chadian	
A. granulatus	Ireland	Tournaisian	Ivorian	
A. portlocki	Ireland	Tournaisian	lower Chadian	
A. gigas	Belgium	Tournaisian	Ivorian	
A. rupinus	USA	Viséan	lower Chadian	middle Osagean
A. tenax n. sp.	USA	Viséan	Arundian	upper Osagean
A. viminalis	USA	Tournaisian	upper Hastarian	upper Kinderhookian
A. cheni	China	Tournaisian		
A. pseudoturgidus	China	Tournaisian		
A.? atlas	China	Tournaisian		
A.? bollandensis	China	Tournaisian		
A.? gilbertsoni	China	Tournaisian		
Amphoracrinus sp.	China	Famennian		

Table 2. Chronostratigraphy of the Mississippian. Correlation of International series, European and North American regional stages, and time bins of Ausich and Kammer (2006) and Kammer and Ausich (2007).



System	International Series	Mississippian Time Bins	European Regional Stages	North American Regional Stages
Mississippian	Serpukhovian	10	Pendelian	Chesterian
	Viséan	9	Brigantian	
		8	Asbian	Meramecian
		7	Holkerian	
		6	Arundian	Osagean
		5	upper Chadian	
	Tournaisian	4	lower Chadian	
		3	Ivorian	
		2	upper Hasterian	Kinderhookian
		1	lower Hasterian	

lenticular bed approximately 28 m above the New Providence Shale Member (Fig. 2).

The Muldraugh Member was a mixed carbonate-siliciclastic, tempestite-dominated ramp environment and the shallow-water equivalent of the Fort Payne Formation in Kentucky and Tennessee (Nicoll and Rexroad, 1975; Peterson and Kepferle, 1970; Kammer and Ausich, 1987; Ausich and Meyer, 1990; Sable and Dever, 1990; Ausich et al., 2000). The Muldraugh Member consists of argillaceous, coarse-grained packstones, yellow-gray dolomitic siltstone, silty dolomite, crinoidal limestone, shale, chert, and geodes (Sable et al., 1966; Kepferle, 1977; Sable and Dever, 1990; Ausich et al., 2000). In the Muldraugh Member, advanced cladids, followed by camerates, dominated in both species richness and the number of specimens (Ausich et al., 2000). Other contemporaneous deltaic localities with a comparably diverse crinoid fauna include the New Providence Shale Member (prodeltaic environments) in southern Indiana and north-central Kentucky (Ausich et al., 1979; Kammer, 1984), the Edwardsville Formation (delta platform environments) in central and southern Indiana (Lane, 1963, 1973; Van Sant and Lane, 1964; Ausich and Lane, 1982), and the Fort Payne Formation of south-central Kentucky (Krivicich et al., 2014 and references cited therein). In other locations, the Muldraugh Member contains a diverse assemblage, including brachiopods, bryozoans, corals (primarily rugosans), conulariids, other echinoderms, gastropods (abundant platyceratids), sponges (abundant hexactinellids), arthropods, trace fossils, and vertebrates (Chondrichthyes teeth and dorsal fin spines). However, in the bed containing *A. tenax*, the only other skeletal elements are crinoid columnals and pluricolumnals.

Figure 1. *Amphoracrinus tenax* n. sp. holotype from the Muldraugh Member (early Viséan) of the Borden Formation, north-central Kentucky. Posterior side of entire specimen. USNM PAL 771320, holotype.

Methods

Table 1 is a list of taxa considered in this study, including their distribution and age. Note that Ausich and Kammer (2008a) designated *A. blairi* Miller and Gurley, 1896a and *A. jessieae* Miller and Gurley, 1896b as nomen dubia; *Amphoracrinus rouchi* Delpey, 1941 was transferred to *Ectocrinus* by Webster et al. (2004); and *A. atlas* (M'Coy, 1849), *A. bollandensis* Wright, 1955, and *A. gilbertsoni* (Miller in Phillips, 1836) are only questionably recognized in China (Webster et al., 2009). In addition, Webster and Waters (2009) described two poorly preserved Devonian crinoids from northwestern China as *Amphoracrinus* sp. These specimens are from the Hongguleleng Formation (Famennian). Unfortunately, both specimens are too poorly preserved to code their morphological characters.

Cluster analyses were conducted using PAST 4.04 (Hammer and Harper, 2006; Hammer et al., 2006). The paired group (UPGMA) algorithm, the Euclidean similarity index, and the no constraints setting were employed to generate dendrograms using the characters listed in Supplemental Tables 1, 2.

Parsimony analyses were performed using PAUP 4.0a168 (Swofford, 2015). Analyses were run using the criterion of maximum parsimony and heuristic searches with random addition repeated 1,000 times. All characters were treated as equally weighted and unordered. Branch swapping was with the tree bisection–reconnection algorithm. Strict consensus, 50% majority rule, and Adams consensus trees were evaluated, the latter to identify potential "wildcard taxa" for possible elimination (Wiley and Lieberman, 2011). The consistency index (ci), retention index (ri), and rescaled index (rc) were calculated, and new trees were generated using rescaled consistency indices. Bayesian, tip-dating method was not attempted because there is insufficient temporal resolution for this approach. Combined, the outgroup taxa span much of the Devonian, but all ingroup species belong to either one or both of two time bins (Tournaisian and Viséan). Tree support was evaluated with bootstrap values, jackknife values, and Bremer support.

Three outgroup taxa are designated. All are from the Periechocrinidae, which were probably ancestors of the Amphoracrinidae (Ausich and Kammer, 2008a, 2008b). Outgroup taxa are *Athabascacrinus orientale* (Waters et al., 2003) (Famennian, China), *Pyxidocrinus collensis* Breimer, 1962 (Emsian, Spain), and *Megistocrinus depressus* (Hall, 1862) (Eifelian-Givetian, United States). Numerous morphological characters were coded; however, based on results of PAUP, only 16 were informative for 14 species of *Amphoracrinus* and three outgroup taxa (Table 1, Supplementary Tables 2, 3). The initial parsimony analysis yielded 1,460 trees with a length of 55. An Adams consensus tree yielded more than one polytomy, and the following five wildcard species were identified and eliminated from further analyses: *A. atlas*, *A. bollandensis*, *A. portlocki* Wright, 1955, *A. rotundus* Wright, 1955, and *A. turgidus* Wright, 1943.

Figure 2. Road cut in Hardin County, north-central Kentucky, where *A. tenax* n. sp. was collected from the Muldraugh Member of the Borden Formation. Lithostratigraphy noted on right; arrow indicates its location on the bench.

With these wildcard taxa eliminated, the resulting analysis yielded 91 trees of length 45. However, as noted, this tree lacked any bootstrap, jackknife, or Bremer support. Next, trees were generated using rescaled consistency indices (rc), resulting in 12 trees of length 26.64722 (Fig. 3.2) that also lacked any bootstrap, jackknife, or Bremer support.

Repository and institutional abbreviation.—The holotype of *A. tenax* n. sp. is deposited in the Smithsonian National Museum of Natural History (USNM), USNM PAL 771320.

Systematic paleontology

The superfamilial classification used here follows Cole (2017), Wright (2017), and Wright et al. (2017); family-level classifications follow Moore and Teichert (1978). Morphologic terminology follows Webster (1974), Ubaghs (1978b), and Ausich et al. (2020b). The plating of interrays is given by the number of plates in each range, from proximalmost plate to the last range before the tegmen. In the posterior interray, the primanal is indicated by "P," and the first interradial plate in regular interrays is indicated by "1." A "?" indicates that more-distal plating is unknown (Ausich, 2021a). Abbreviations used in designating measurements include the following: CrH, crown height; CaH, calyx height; CaW, calyx width; CoH, column height. An * indicates a measurement was incomplete.

Class Crinoidea Miller, 1821
Subclass Camerata Wachsmuth and Springer, 1885
Infraclass Eucamerata Cole, 2017
Order Monobathrida Moore and Laudon, 1943
Suborder Composocrinina Ubaghs, 1978a
Superfamily Periechocinacea Bronn, 1849
Family Amphoracrinidae Bather, 1899
Genus *Amphoracrinus* Austin, 1848

Type species.—*Amphoracrinus gilbertsoni* Miller in Phillips, 1836.

Included species.—*A. atlas* (M'Coy, 1849); *A. bollandensis* Wright, 1955; *A. cheni* Webster et al., 2009; *A. compressus* Wright, 1943; *A. crassus* (Austin and Austin, 1843); *A. gigas* Austin in Wright, 1955; *A. gilbertsoni* (Miller in Phillips, 1836); *A. granulatus* (Austin and Austin, 1843); *A. portlocki* Wright, 1955; *A. pseudoturgidus* Chen and Yao, 1993; *A. rotundus* Wright, 1955; *A. rugosus* (Rofe, 1865); *A. rupinus* Webster and Lane, 1987; *A. tenax* n. sp.; *A. turgidus* Wright, 1943; and *A. viminalis* (Hall, 1863).

Amphoracrinus tenax new species
Figures 1, 4

Type.—The holotype of *A. tenax* n. sp. is designated USNM PAL 771320.

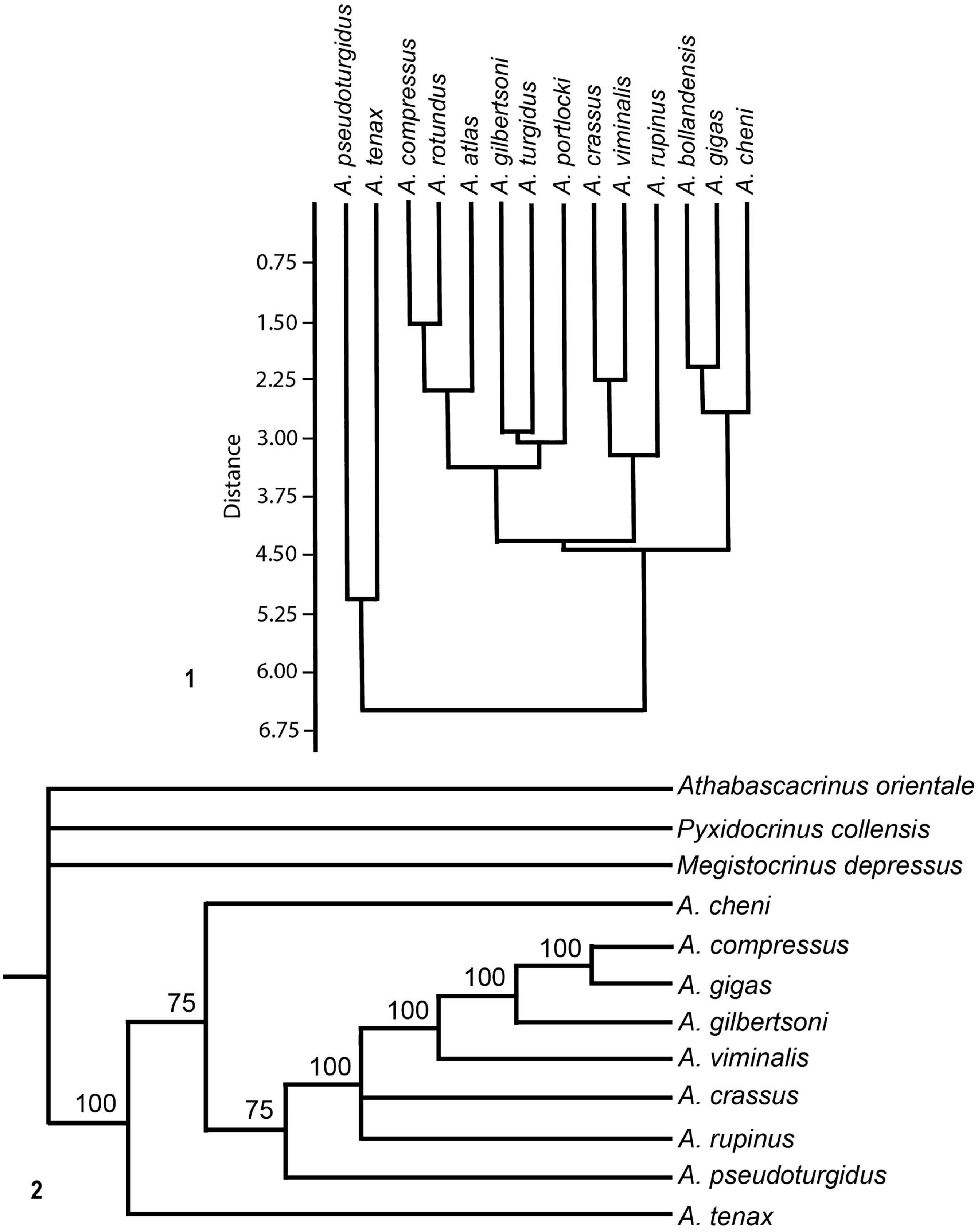


Figure 3. Results from morphological analyses of *Amphoracrinus*. (**1**) Dendrogram from cluster analysis of morphological characters of *Amphoracrinus* species. (**2**) A 50% majority-rule tree of nine species of *Amphoracrinus* with three outgroup taxa. Values at nodes indicate the percentage of most parsimonious trees that recovered that relationship (data in Supplemental Tables 1, 2, 3).

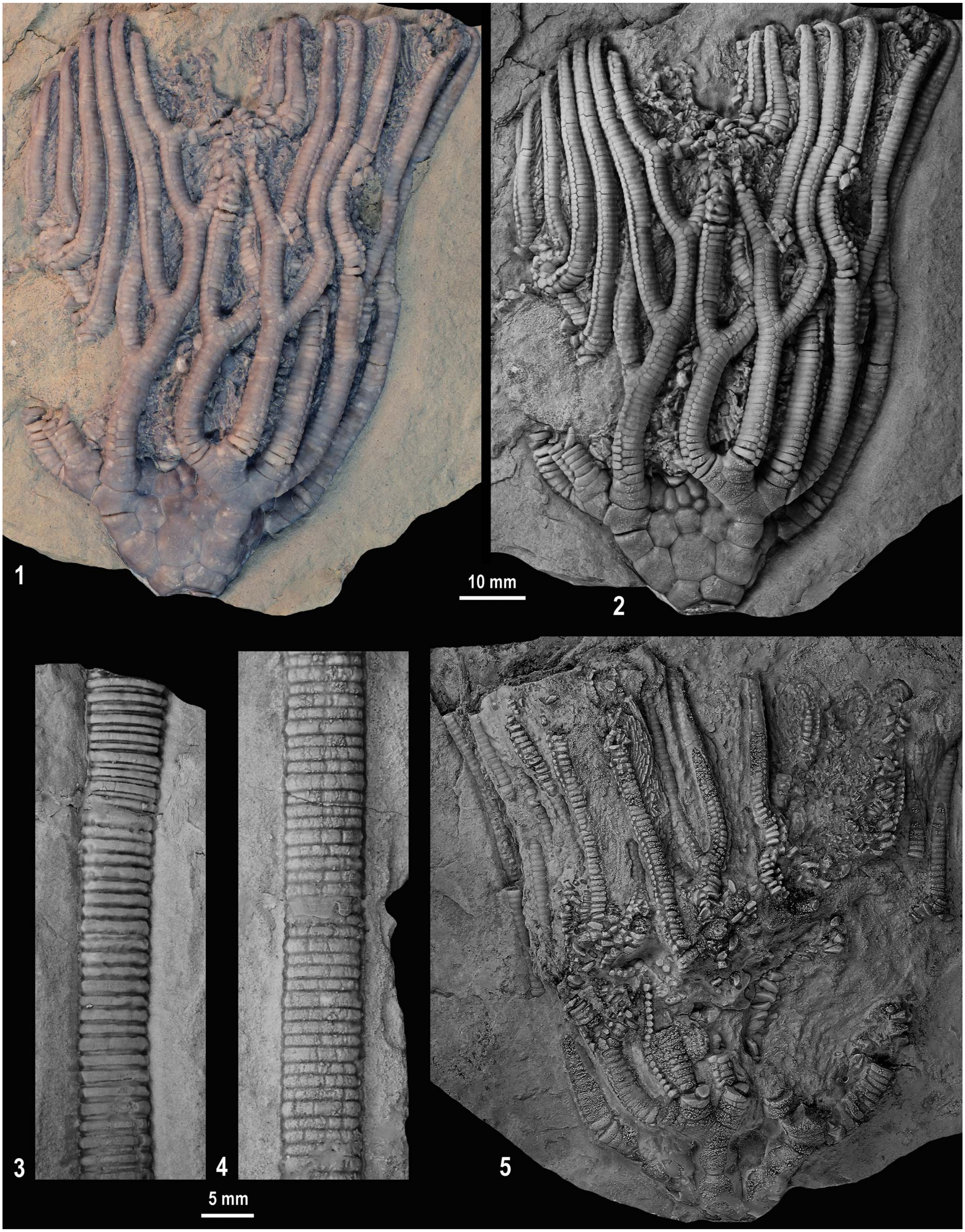


Figure 4. Holotype of *A. tenax* n. sp. USNM PAL 771320. (**1, 2**) Well-articulated posterior side of the crown; (**3**) proximal portion of column, compare with Figure 1; (**4**) portion of middle column, compare with Figure 1; (**5**) poorly articulated anterior side of crown. (**2–5**) Coated with ammonium chloride.

Diagnosis.—Calyx low cone shape; calyx plates convex, smooth; basal circlet 20% of calyx height, ridge at base of calyx absent; radial plates as high as wide, unequal in size, smaller than primanal; three interradial plates in regular interrays with distalmost range adjacent to primibrachials, regular interrays depressed; first fixed primibrachial tetragonal, as high as wide; CD interray very much wider than other regular interrays, three plates above primanal; first primibrachial smaller than radial plate and primaxil, more than five CD-interray plates in calyx; two fixed primibrachials, 15–20 free arms project upward and branch.

Occurrence.—Muldraugh Member of the Borden Formation, Hardin County, north-central Kentucky, 37°48′23.492″N, 85° 49′29.513″W, UTM 16N 591623 4184859.

Description.—Calyx medium sized, low cone shape (Fig. 4.1), ~0.52 times higher than wide; arms grouped and interrays moderately depressed; calyx plates low convex shape, smooth plate sculpturing. Basal circlet high, visible in side view, ~20% of calyx height (Fig. 4.2); three basal plates, unequal in size, wider than high, much smaller than radial plates. Radial circlet ~35% of calyx height; radial plates five, hexagonal, as high as wide. Regular interrays narrowly in contact with tegmen, all plates convex as noted; first interradial hexagonal, as high as wide, smaller than radials and first primibrachial; plating in second range unknown. Primanal heptagonal, higher than wide, largest plate in calyx, interrupts the radial circlet; plating in CD interray P–3–5–? (Fig. 4.2), plates have impressed sutures; second range of interradial plates in posterior with subtle plate plications that are ridges that connect with like ridges on adjoining plates (radials, primanal, first and second primibrachials, adjacent plates in the first and second ranges of interradial plates, and some plates of the third range of posterior interray plates) (Fig. 4.2). CD interray in contact with tegmen. First primibrachial tetragonal or pentagonal, approximately as high as wide, convex, smaller than radial plates and primaxil; second primibrachial axillary, approximately twice as wide as high. Intrabrachial plates between adjacent half-rays absent. Tegmen not visible.

Three or four free arms per ray (C ray four arms; A and D rays three arms). Free arms begin with first tertibrachial, first tertibrachial either uniserial or biserial (Fig. 4.2); all subsequent brachials biserial. Free arms robust, aborally rounded; directed obliquely upward, narrow distally, and abaxially incurved at distal end of crown. Each free arm may have as many as four branches (Fig. 4.2), with branching pattern variable above the first branch (may be either endotomous or exotomous) (Fig. 4. 2). Pinnules slender. Column circular (Figs. 1, 4); in proximal column heteromorphic (N212 pattern), latus of nodals very convex and latus of internodals progressively less convex (Fig. 4.3); mesistele with very subtle N212 pattern and some places approach homeomorphy, latus of columnals convex (Fig. 4.4).

Etymology.—The name, *tenax* (m), is Latin for steadfast or tenacious.

Measurements.—CrH, 90.0; CaH, 25.0*; CaW, 12.0; CoH, 230*.

Remarks.—USNM PAL 771320 is the most complete known specimen of this genus. Most species are known from only the theca (calyx and tegmen). Because the arms are largely complete, they hide the tegmen, so comparison to other species is limited to characters of the calyx.

Amphoracrinus tenax n. sp. differs from other North American species because *A. rupinus* has a very low cone shape, coarsely granulose plate sculpturing, a continuous ridge around the base of the calyx, radial plates wider than high and the largest plates in the calyx, most-distal plates in calyx interrays that abut secundibrachials, first primibrachial wider than high, CD interray wider than other interrays, three or four extra plates in the CD interray, and 10 free arms. By contrast, *A. viminalis* has a very low bowl-shaped calyx, coarsely granulose plate sculpturing, a broken ridge around the base of the calyx, radial plates wider than high and the largest plates in the calyx, distal-most interradials in calyx that abut secundibrachials, first primibrachial wider than high, CD interray wider than other interrays, two plates above the primanal, and 10 free arms (see Supplemental Table 5 for comparison with other species).

Results and discussion

Paleogeography and evolution.—*Amphoracrinus viminalis*, the oldest named species, is from northeastern Ohio from the Meadville Shale Member of the Cuyahoga Formation and dates to the late Kinderhookian (Tournaisian, late Hastarian) (Table 1). The Meadville Shale was deposited in a shallow marine deltaic tempestite shelf setting that resulted in excellent crinoid preservation (Ausich and Roeser, 2012; Kammer and Roeser, 2012). *A. rupinus* (Webster and Lane, 1987) is from southern Nevada (Meadow Valley Range) from the Anchor Limestone of the Monte Cristo Group (early Osagean, Tournaisian, Ivorian), where monobathrid camerates were the dominant element of the crinoid fauna (Webster and Lane, 1987). *A. rupinus* was also documented in New Mexico from the Nunn Member of the Lake Valley Formation (early Osagean/late Tournaisian) (Rhenberg and Kammer, 2013). The Nunn Member in general was a narrow and relatively deepwater low-energy carbonate ramp with Waulsortian mounds; however, the specific location where *Amphoracrinus* occurred was from a shallower shelf subenvironment comparable to the Burlington Shelf (Rhenberg and Kammer, 2013). *Amphoracrinus tenax* n. sp. is now the youngest (early Viséan, Arundian) described species of *Amphoracrinus*.

Amphoracrinus is best known from Western Europe, where it occurs from the Tournaisian (Ivorian) to the early Viséan (upper Chadian) in England, Wales, Ireland, and Belgium. In Ireland, *Amphoracrinus* is present in the Hook Head Formation (Tournaisian, Ivorian), particularly the shallow-water "Michelinia Beds" (Ausich and Sevastopulo, 2001), which was a mixed carbonate and siliciclastic tempestite shelf-ramp (Ausich and Sevastopulo, 1994). It is also present in the equivalent ramp setting in southwestern United Kingdom. *Amphoracrinus* was a dominant faunal element in the Tournaisian (lower Chadian) to the Viséan (upper Chadian) Waulsortian-related facies in England, Wales, Ireland, and Belgium (Wright, 1955; Ausich and Sevastopulo, 1994, 2001; Ausich and Kammer, 2006, 2008a; Donovan et al., 2006).

As noted, the oldest occurrence of *Amphoracrinus* is from the Famennian of China (Webster and Waters, 2009). Chen and Yao (1993) described *A. atlas*, *A. bollandensis*, *A. gigus*, *A. gilbertsoni*, and *A. pseudoturgidus* from the Tournaisian of China. These species assignments were revisited by Webster et al. (2009), who described *A. cheni* and *A. pseudoturgidus*; but they recognized the occurrences *A. atlas*? and *A. gilbertsoni*? as questionable. Both the Famennian and Tournaisian occurrences in China are interpreted to have been from shallow-water habitats with no clear evidence of association with carbonate buildups.

Cluster analysis was performed on morphological characters (Supplemental Tables 1, 2) to identify any morphological similarities among *Amphoracrinus* species within and between geographic areas. In the resultant dendrogram, the three North American species are not grouped together. *Amphoracrinus tenax* n. sp. and *A. pseudoturgidus* form a group at the base of the dendrogram, and *A. crassus*, *A. rupinus*, and *A. viminalis* form a group (Fig. 3.1). *Amphoracrinus bollandensis*, *A. gigas*, and *A. cheni* group together, and the remaining Western European species (with *A. rupinus* and *A. viminalis*) group together in various clusters.

Phylogenetic analyses were also performed. Whereas the phylogenetic tree in Figure 3.2 cannot be demonstrated to be a robust phylogenetic solution, it displays interesting relationships, with European, North American, and Chinese species intermixed. For example, *A. tenax*, *A. cheni*, and *A. pseudoturgidus* (Tournaisian, China) are ladderized at the base of the ingroup (Fig. 3.2). By contrast, the two other North American species (*A. viminalis*, Tournaisian, and *A. rupinus*, Viséan) are in a clade with all European species. *Amphoracrinus rupinus* and *A. crassus* are in the crownward clade and are on a polytomy. *A. viminalis* is in a basal position of the crownward group. Thus, the three North American species are in reverse stratigraphic order and are associated with species of contrasting paleogeographies. Interpretation of the phylogenetic analysis (Fig. 3.2) is regarded as tentative, but the repeated recovery of relationships at the base of the tree suggest that these taxa have close phylogenetic and paleogeographic relationships. The older species of North American *Amphoracrinus* (*A. rupinus* and *A. viminalis*) are most closely associated with European species, whereas the youngest North American species (*A. tenax* n. sp.) is more closely associated with species from China, which may suggest either separate paleogeographic origins or multiple migration events for North American members of this genus. These relationships will not be resolved until characters of the tegmen, arms, and column are known for most species, which is unlikely. At least tegmen characters for *A. tenax* may become known with additional specimens, which is significant because tegmen characters are highly variable and phylogenetically important (Kammer et al., 2013; Ausich and Kammer, 2016).

Ausich and Kammer (2013) evaluated the temporal and paleogeographic patterns among Mississippian crinoids in North America and Western Europe. On the basis of analyses of first occurrences of genera, paleobiogeography through the history of a genus, and biodiversity changes through the Mississippian, Ausich and Kammer (2013) concluded that the evolutionary center of monobathrid camerate crinoids, disparid crinoids, and cyathocrine crinoids was predominantly in North America, with subsequent migration to Western Europe. A major factor driving migration was interpreted to be sea-level rise following the late Kinderhookian glaciation (Walker et al., 2002; Caputo et al., 2008; Kammer and Matchen, 2008). Waters et al. (2008) and Webster et al. (2009) concluded that most Chinese Mississippian crinoids migrated from Western Europe. Thus, it follows that the Tournaisian crinoid faunas from China were originally seeded by migration from North America and Europe as a result of sea-level rise following late Kinderhookian glaciations.

With *Amphoracrinus* sp. (Webster and Waters, 2009) (Famennian) assigned to *Amphoracrinus*, a more-nuanced paleogeographic history must have existed. Origination of *Amphoracrinus* in northwestern China during the Famennian would be consistent with the overall conclusions of several studies that indicate that Famennian blastoids and crinoids in China have close affinities to early Mississippian crinoids in North America (Lane et al., 1997; Waters et al., 2003, 2008; Webster and Waters, 2009). This would suggest that during the latest Devonian and earliest Mississippian, migration routes were more freely open than traditionally understood between China, North America, and Western Europe, including westward migration.

A potential history of *Amphoracrinus* is that this genus originated during the Late Devonian of China, where it thrived in shallow-water, nonbuildup-associated habitats. It then migrated westward, with the first preserved occurrence in western Laurussia (North America) in a siliciclastic deltaic setting (*A. viminalis*) and the first occurrence in central Laurussia (Western Europe) in a mixed carbonate–siliciclastic setting (*A. crassus*, *A. granulatus*, and *A. gigas*) (Table 1). Younger species in China and North America persisted in mixed carbonate–siliciclastic settings, whereas in Western Europe, *Amphoracrinus* thrived in facies associated with Waulsortian mudmounds as well as other settings. As noted, the morphological and phylogenetic analyses suggest that migratory pathways were open throughout the Famennian–Viséan interval.

To better resolve the paleogeographic history of *Amphoracrinus,* a more-detailed understanding of *Amphoracrinus* sp. from the Famennian of China is required, as well as more occurrences of the genus from both the late Devonian and Tournaisian. Analyses of multiple clades through this interval are also needed to more fully understand this important episode in crinoid evolutionary history.

Taphonomy.—*Amphoracrinus tenax* n. sp. is an illustrative example of the earliest phases of disarticulation of a robust camerate crinoid. Preservation of two sides of this specimen are strikingly different (Fig. 4.2, 4.5). This preservational contrast is well known for many clades with multielement skeletons (e.g., see Brett and Baird, 1986 and Meyer and Milsom, 2001 for discussions on this phenomena). This style of preservation has been noted for Paleozoic (Meyer et al., 1981; Brett and Baird, 1986) and Mesozoic (Springer, 1901; Struve, 1957; Seilacher et al., 1968; Hagdorn, 1978, 1998; Neugebauer, 1978; Simms, 1986; Milsom et al., 1994; Hess, 1999) crinoids.

Brett and Baird (1986) discussed this differential preservation in the Silurian camerate crinoid *Eucalyptocrinites* Goldfuss, 1831. In this Silurian crinoid, arms were preserved mostly intact on the lower surface, but arms were absent from the upper surface. In both cases, calyx plates were present but displaced due to compaction.

The *A. tenax* (Figs. 1, 4) holotype USNM PAL 771320 is important for understanding the taphonomy of the crown and the significant height of the column. Further, this allows consideration of relative disarticulation of nearly the entire skeleton of a crinoid inferred to have had only ligamentary articulations. The CD interray is very well preserved, whereas the opposite side (A ray) is in a much more advanced stage of disarticulation. The A ray was the stratigraphically up side when this specimen was found (Fig. 4.1, 4.2). On the A-ray side, the radial plates and fixed brachials remain firmly sutured, but the interradial plates are slightly askew (Fig. 4.5). Every free arm is disarticulated from the calyx. Most of the preserved arms are in approximately the correct position, but the biserial brachials are beginning to separate along some arm segments. In other places, brachials are completely disarticulated but remain as part of the specimen. Pinnules are in the correct position and articulated, in their correct position but slightly askew, or completely disarticulated. By contrast, the CD interray, the stratigraphically down side of the specimen, was buried in the sediment. Calyx plates are sutured; all free arms are in place, with three having minor displacement (Fig. 4.1, 4.2). Proximal arms are mostly intact, but in the middle and distal parts of the arms some disarticulation is present. However, the distal, narrower, incurled arms are intact. A few pinnules are intact, but they are mostly disarticulated. Pinnules may be approximately in place or completely disarticulated. The proximal and middle column are completely articulated, but the distal column is absent (Figs. 1, 4.3, 4.4)

Actualistic studies of disarticulation and preservation have been conducted with articuliform crinoids that have muscles in their arms, and muscles are the most rapidly decaying tissue (Meyer, 1971; Liddell, 1975; Meyer and Oji, 1992). By contrast, Mississippian camerate crinoids are inferred to have had only ligamentary connective tissues, on the basis of both brachial articulations and disarticulation patterns (e.g., Lane and Burke, 1976; Ausich and Baumiller, 1993).

A possible scenario for the preservation of USNM PAL 771320 is that the crown and 230 mm of the column broke away from the more-distal column, presumably by a storm or gravity flow (Taylor and Brett, 1996). The crinoid was transported some unknown distance and was only partially buried. The enclosing matrix is uniformly fine grained, so if it was displaced by a storm or gravity flow it was likely transported in the upper, finer-grained portion of the resulting deposit, as discussed by Ausich and Meyer (1990), Taylor and Brett (1996), and Ausich (2021b). The upper, more-exposed surface decayed and disarticulated more rapidly, and the lower buried surface may have decayed more slowly. The specimen was eventually permanently buried before it was completely disarticulated. Current action did not disperse skeletal elements, and it does not appear to have been significantly attacked by scavengers. However, note the lack of plates on the lower arms (left side of Fig. 4.1, 4.2 and the opposite side of Fig. 4.5). It is possible that after burial, this specimen was disturbed by a burrowing organism (Maples and Archer, 1989) (other trace fossils occur in this unit). Thus, although buried and intact, all connective tissues had decayed. Finally, the specimen was compacted and lithified, yielding its present condition (Figs. 1, 4).

The poor articulation on the upper surface was either a reflection of differential disarticulation on the seafloor or a reflection of differential decay of connective tissues and disarticulation manifested by compaction. Overall, the pinnules are the elements displaying the most disarticulation, followed by the arms, calyx, and column. Camerate calyx plates are traditionally considered to have been cemented to one another more than in other clades during life (e.g., Ubaghs, 1978a); however, their more-secure articulations may have been due to stereom interlocking (Gorzelak et al., 2012; Ausich, 2021b). The difference in disarticulation propensity of pinnules, arms, and column may be the result of surface area of ligamentary articulations, with the smaller pinnular facets more likely than the larger brachial facets to disarticulate. The largest ligamentary articulations between columnals are all intact. This result is consistent with studies by Allison (1990) and Breton (1997), who concluded that disarticulation rates among asteroid clades were also correlated with plate size and robustness.

During decay of a dead extant crinoid, Meyer and Oji (1992) convincingly demonstrated that some sort of a microbial sheath was responsible for the excellent preservation of slabs of *Uintacrinus socialis* Grinnell, 1876, which includes numerous specimens with the down sides very well preserved and the up-side plates disarticulated. Crinoid preservation enhancement by microbial sheaths has been hypothesized in other examples of exceptional preservation (e.g., Seilacher et al., 1985). It is not possible to determine whether a microbial sheath enhanced the preservation of this Muldraugh Member crinoid because, if present, a microbial sheath would not be likely to have been preserved in sediments that lack any evidence of having been anoxic.

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Data availability statement

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.jq2bvq889.

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