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CAMERATE AND DISPARID CRINOIDS FROM THE LATE KINDERHOOKIAN MEADVILLE SHALE, CUYAHOGA FORMATION OF OHIO

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ABSTRACT—Crinoids were first reported from the Cuyahoga Formation in northeastern Ohio by James Hall in 1863. However, these crinoids have not been re-examined in detail since the late nineteenth century. With the restudy of classical and more recent collections, ten (nine camerate and one disparid) species-level taxa are recognized from the late Kinderhookian Meadville Shale Member, Cuyahoga Formation, including the camerates *Amphoracrinus viminalis* (Hall, 1863); *Aorocrinus helice* Hall, 1863; *Aorocrinus meyeri* n. sp.; *Aryballocrinus martini* n. sp.; *Cusacrinus daphne* (Hall, 1863); *Platycrinites* s.l. *contritus* (Hall, 1863); *Platycrinites* s.l. *graphicus* (Hall, 1863); *Platycrinites* s.l. *lodensis* (Hall and Whitfield, 1875); and *Platycrinites* s.l. *burkei* n. sp. In addition, *Halysiocrinus* sp. is the first disparid reported from this fauna. *Platycrinites* s.l. *bedfordensis* (Hall and Whitfield, 1875) is designated a *nomen dubium*. Growth is evaluated for *Aorocrinus helice* and *Cusacrinus daphne*, which had contrasting development. The growth of the *Aorocrinus helice* calyx was largely not allometric but that of the primaxil plate was, suggesting the arms may have grown allometrically. In contrast, much of the calyx of *Cusacrinus daphne* displayed allometric growth.

INTRODUCTION

JAMES HALL (1863) was the first to report lower Mississippian crinoids from northeastern Ohio. Subsequently, this fauna received very little study until E. W. Roeser (1986) made new collections as part of his M.S. thesis research at the University of Cincinnati. These crinoids are now recognized as being from what is now the Meadville Shale Member of the Cuyahoga Formation (late Kinderhookian; Tournaisian (TN2), late Hastarian). Further, Gary Meszaros, an amateur paleontologist, collected additional new material during the 1970s (see Kammer and Roeser, 2012). Reconsideration of Cuyahoga crinoids is warranted because of the large, new collections made by E. W. Roeser and Gary Meszaros. A greater number of specimens allows for consideration of intraspecific variability, aspects of ontogeny, and description of these crinoids, including new taxa. The presence of *Amphoracrinus* in the Cuyahoga Formation is the oldest known occurrence of this genus. *Halysiocrinus* is known from the Devonian, but the Meadville Shale is its oldest occurrence in Mississippian strata. In addition, three new species are reported here, *Aorocrinus meyeri* n. sp., *Aryballocrinus martini* n. sp., and *Platycrinites burkei* n. sp. In this study, we consider only camerate and disparid crinoids. Kammer and Roeser (2012) will consider cladid crinoids from this fauna.

OCCURRENCE AND FAUNAL RELATIONSHIPS

Meadville Shale crinoids are known from Summit County, Ohio, near Richfield. Crinoids occur predominantly in thin, lenticular siltstone beds of this lithostratigraphic sequence, which is dominated by shale. The collection by Roeser (housed in the Cincinnati Museum Center) is from the upper part of the Meadville Shale Member of the Cuyahoga Formation (Roeser, 1986). It is from a creek exposure in the northern part of Richfield township, Summit County, Ohio (Lat. N 41°14′52.6″, Long. N 81°38′22.6″). The Meszaros collection is from an undetermined position within the Meadville Shale. This material is from a creek exposure and near Lodi, Medina County, Ohio (Lat. N 41°01′26″, Long. N 82°04′33″) (Google Earth). The Meadville Shale Member of the Cuyahoga Formation is late Kinderhookian in age (time bin 2 of Ausich and Kammer, 2006 and Kammer and Ausich, 2007).

Aorocrinus helice (Hall, 1863) is the most abundant crinoid in the Meadville Shale fauna, but other camerate crinoids are relatively rare. In the fauna from Richfield township, Roeser (1986) noted that the camerates *A. helice* and *Cusacrinus daphne* had the greatest rank abundance and had three and two times, respectively, the abundance of other camerates. Camerates are considerably less diverse than cladid crinoids (see Kammer and Roeser, 2012). All camerate crinoid species reported here are endemic to the Meadville Shale. These species belong to genera that range through at least the Kinderhookian and/or Osagean. *Aorocrinus* and *Cusacrinus* are endemic to North America, whereas *Amphoracrinus*, *Aryballocrinus*, and *Platycrinites* s.l. are known outside of Laurentia. The lone disparid, *Halysiocrinus*, is known with certainty only on Laurentia.

In North American, Kinderhookian crinoid assemblages, the occurrence of camerate crinoids and camerate genus richness are variable. The average camerate genus richness in a Kinderhookian assemblage is 6.6 (range, 2 to 12), so the four genera in Meadville Shale is low. The four most commonly represented families in these faunas are the Dichocrinidae, Rhodocrinitidae, Platycrinitidae, and Actinocrinitidae. Only the latter two families occur in the Meadville Shale, along with the Periechocrinidae. Among genera, the Meadville Shale fauna contains three common taxa, *Aryballocrinus*, *Cusacrinus*, and *Platycrinites*, but *Amphoracrinus* is not know from elsewhere in the Kinderhookian of North America. Although there are important differences, the Meadville Shale fauna most closely resembles that of the Wassonville Formation (Gahn and Baumiller, 2004).

The Meadville Shale has a high diversity of cladid crinoids (Kammer and Roeser, 2012), which is consistent with the dominance of cladids in Osagean siliciclastic facies (Ausich et al., 1979; Kammer and Ausich, 1987). With the Osagean expansion of carbonate ramps, Mississippian carbonate habitats were dominated with a high abundance and diversity of camerate crinoids (Kammer and Ausich, 2006).

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FIGURE *1*—*Amphoracrinus viminalis* (Hall, 1863), A-ray lateral view of crown, CMCIP 46132, ×2.0.

SYSTEMATIC PALEONTOLOGY

Terminology follows Ubaghs (1978a) with modifications from Ausich et al. (1999). The scheme for defining relative proportions of the calyx follows Ubaghs (1978a, fig. 72). Repositories are indicated as follows: CMCIP, Cincinnati Museum Center, Cincinnati, Ohio; CMNH Cleveland Museum of Natural History; OSU, Orton Geological Museum, Ohio State University; and NYSM, New York State Museum, Albany.

Carboniferous chronostratigraphy follows Heckel and Clayton (2005). The detailed chronostratigraphic scheme and correlations follow Ausich and Kammer (2006).

All crinoids considered here are from the Meadville Shale, Cuyahoga Formation in northeastern Ohio. Examined specimens are from a number of localities discovered in the past few decades. For further information on these locations, the reader is referred to the museums that house these specimens. All measurements are in mm; * denotes an incomplete measurement or measurement of a compressed specimen; V** denotes holotype, neotype, or lectotype.

Allometry measurements and statistics used the linear model function of the Paleontological Data Analysis software (Hammer and Harper, 2006).

Class CRINOIDEA Miller, 1821
Subclass CAMERATA Wachsmuth and Springer, 1885
Order MONOBATHRIDA Moore and Laudon, 1943
Suborder COMPSOCRININA Ubaghs, 1978b
Superfamily PERIECHOCRINOIDEA Bronn, 1849
Family AMPHORACRINIDAE Bather, 1899
Genus AMPHORACRINUS Austin, 1848

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

AMPHORACRINUS VIMINALIS (Hall, 1863)
Figures 1, 2, 3.1, 3.2, 4

Actinocrinus viminalis HALL, 1863, p. 54; HALL, 1864, p. 54; SHUMARD, 1868, p. 350; HALL AND WHITFIELD, 1875, p. 165, pl. 11, figs. 12–14; MILLER, 1889, p. 220; WELLER, S., 1898, p. 83.

Amphoracrinus viminalis (HALL, 1863). MILLER, 1889, p. 223, fig. 244; MILLER, 1897, p. 734; WACHSMUTH AND SPRINGER, 1897, p. 590, pl. 54, fig. 8; WELLER, 1898, p. 83; BASSLER AND MOODEY, 1943, p. 300; WEBSTER, 2003; AUSICH AND KAMMER, 2008, p. 1142.

Displodocrinus viminalis (HALL, 1863). WEBSTER AND LANE, 1987, p. 25.

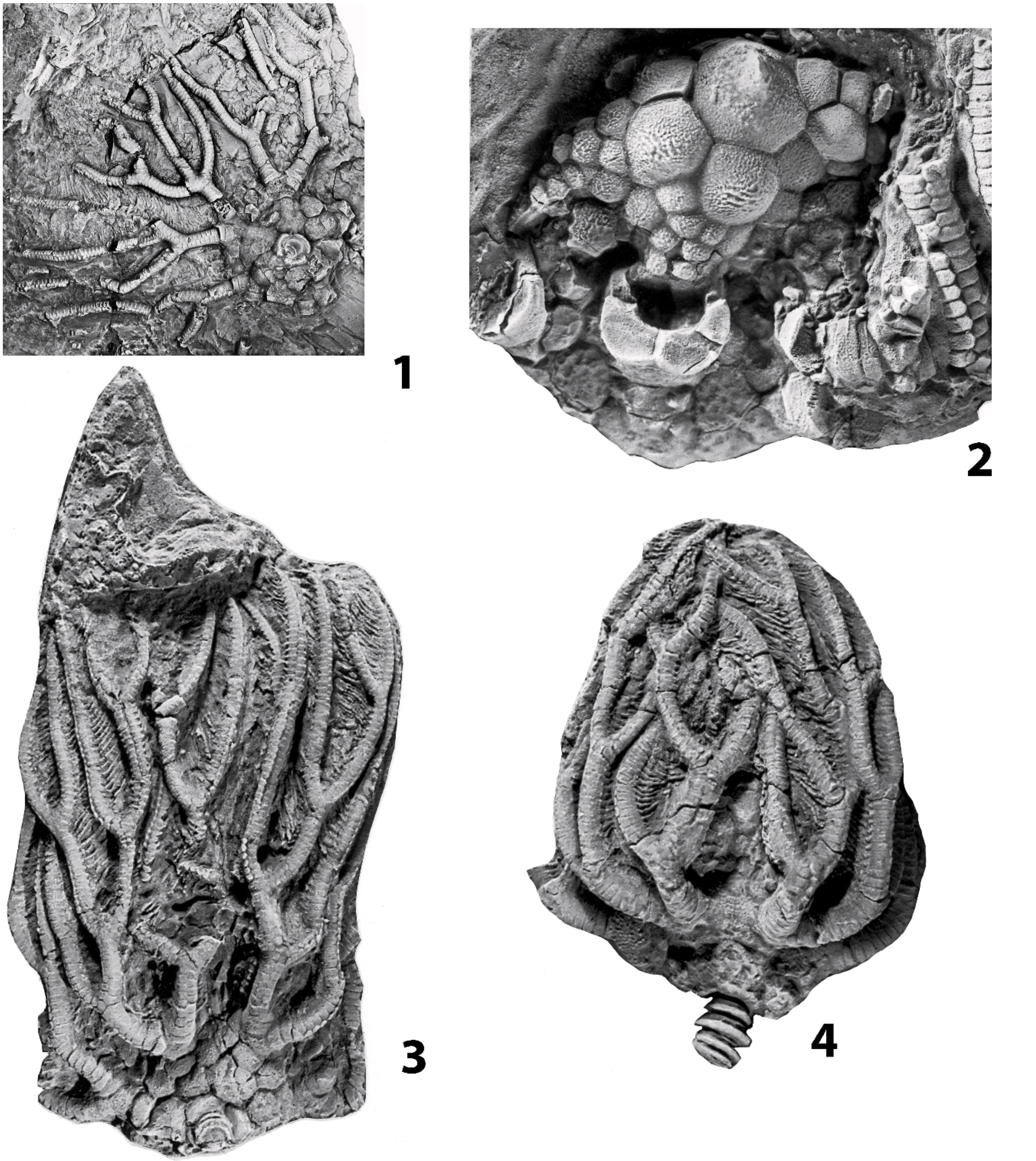

FIGURE 2—*Amphoracrinus viminalis* (Hall, 1863). *1*, partial crown, holotype, NYSM 6117 (previously figured in Hall and Whitfield, 1875, pl. 11, fig. 13), ×1.0; *2*, oblique view of tegmen, CMCIP 46134, ×4.0; *3*, A-ray lateral view of crown with *Platyceras* gastropod CMCIP 46131, ×1.5; *4*, EA interray lateral view of crown (compare to *Fig. 2.2*) CMCIP 46130, ×1.5.

Diagnosis.—Calyx low cone to bowl shape; calyx plates convex; basal circlet a flat cone visible in lateral view; radial plate approximately 1.5 times wider than high; first primibrachial a little smaller than both the radial and primaxil; 10 free arms that branch.

Description.—Calyx medium, low cone to bowl (Fig. 1), approximately twice as wide as high; arms grouped and interrays moderately depressed; calyx plates low convex shape, on well-preserved specimens sculpturing irregular and coarsely nodose, calyx plates relatively thick. Basal circlet very low cone, truncate proximally with slight protuberance over proximal column, visible in side view, approximately 15 percent of calyx height; basal plates three, unequal in size, approximately one-half size of radial plates. Radial circlet approximately 20 percent of calyx height; radial plates five, hexagonal in A, C, and D rays, heptagonal in B and E rays,

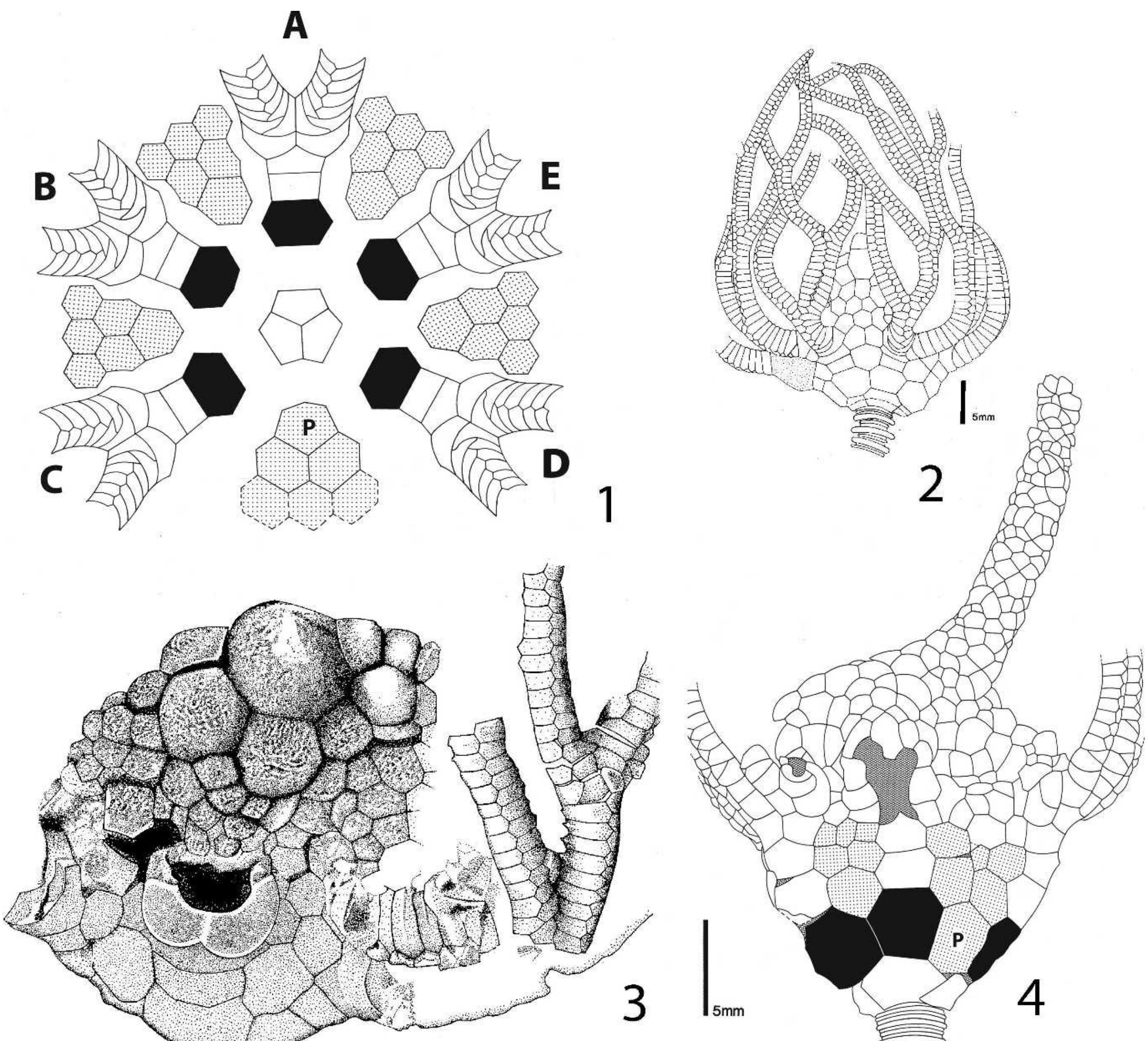

FIGURE 3—*Amphoracrinus viminalis* (Hall, 1863) and *Cusacrinus daphne* (Hall, 1863). *1–3, A. viminalis: 1*, plate diagram, A–E designation of rays; P, primanal; black, radial plates; stippled, fixed interradial plates; *2*, EA interray lateral view of crown, CMCIP 46130 (compare to *Fig. 1.4*), scale as indicated; *3*, stippled drawing of oblique view of tegmen (compare to *Fig. 1.2*), CMCIP 46134, approximately ×4.0; *4*, *C. daphne*, C-ray lateral view of calyx (compare to *Fig. 8.1*), CMCIP 46108, scale as indicated.

approximately 1.6 times wider than high, mean height-width ratio 0.65. Regular interrays in contact with tegmen, all plates convex as noted above; first interradial hexagonal, approximately as high as wide, smaller than radials and slightly larger than first primibrachial. Second range in calyx with two additional plates approximately as high as wide (Fig. 1), third range with three plates and in contact with tegmen (Fig. 2.1). Primanal hexagonal or heptagonal, slightly higher than wide, sculpturing like radials, higher than and slightly narrower than radial plates, interrupts the radial circlet; plating in CD interray P-2-3 or rarely P-3-3 (Fig. 2.1); CD interray in contact with tegmen.

Fixed brachials few. First primibrachial tetragonal or hexagonal, approximately twice as wide as high, convex, smaller than radial plates and primaxil; second primibrachial axillary approximately twice as wide as high, pentagonal. First secundibrachial tetragonal, uniserial, wider than high, strongly convex; each pair of first secundibrachials in ray in sutural contact medially. All subsequent brachials biserial, distal-most fixed brachial first or second secundibrachial. Intrabrachial plates between adjacent half-rays absent. Tegmen hidden or compressed on available specimens but probably approximately 2.0 times as high as calyx height (Figs. 2.4, 3.2); convex sides from arm openings to summit; plates medium sized, flat to low convex, summit with four orals with irregularly and coarsely nodose sculpturing (Figs. 2.1, 3.2, 3.3), surrounding large, spinose CD oral; details of anal tube not known. Ten arms where they become free above the calyx, become free on first secundibrachial (Fig. 1). All free brachials biserial. Free arms robust, aborally rounded; directed laterally at base then upward, narrow distally; each free arm may have as many as four branches (Fig. 4), but branching pattern is variable above

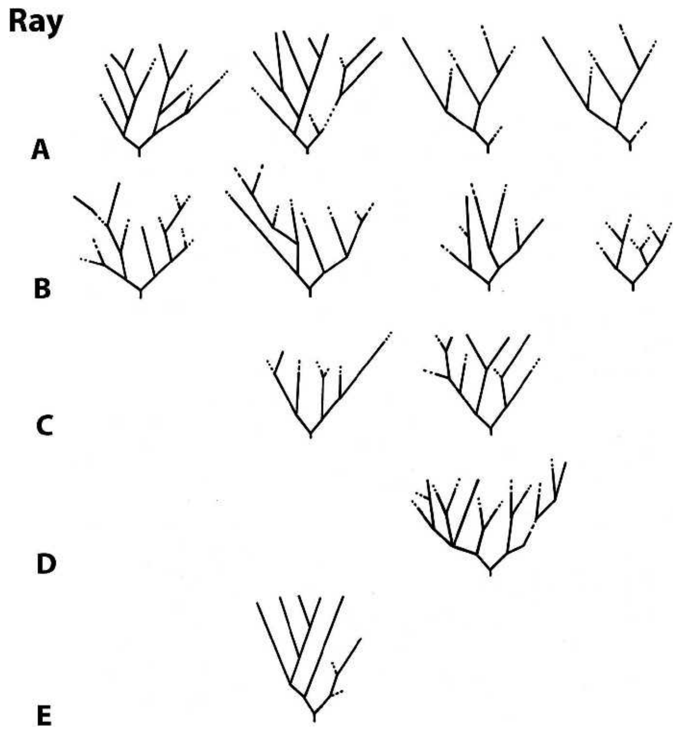

FIGURE 4—Variations in arm branching patterns by ray for *Amphoracrinus viminalis* (Hall, 1863b).

the first branch (Figs. 2.1, 2.3, 2.4, 3.2). Pinnules long, slender, keel along aboral surface. Column circular, heteromorphic; in proximal column N212 pattern. Columnals circular, latera of nodals very convex (Figs. 2.4, 3.2), priminternodals convex, secundinternodals nearly flat. Lumen small pentalobate.

Material examined.—Holotype of *Amphoracrinus viminalis* NYSM 6117 from Richfield. Additional Richfield specimens: CMCIP 46093b; 46099; 46102; 46130–46135; 46138; and 46140–46142. Lodi specimens: CMNH 5224; 5824; 5826a, 5826b; 5897; 9513b; 9521; and 12264.

Occurrence.—*Amphoracrinus viminalis* from the Meadville Shale Member of the Cuyahoga Formation in northeastern Ohio at Lodi and Richfield.

Discussion.—Although named in 1863, the first illustrations of *A. viminalis* were by Hall and Whitfield (1875, pl. 11, fig. 13). A second specimen, which has not been located, was also illustrated by Hall and Whitfield (1875, pl. 11, fig. 12). NYSM 6117 is regarded as the holotype by the New York State Museum, and this is followed here.

The identification of the genus *Amphoracrinus* in North America has been problematic (Ausich and Kammer, 2008). However, Ausich and Kammer (2008) recognized two North American species, *A. viminalis* and *A. rupinus* Webster and Lane, 1987 (from the Anchor Limestone of Nevada). This study confirms that *A. viminalis* is the oldest recognized species of this important European genus. Both North American occurrences are relatively old for the genus with *A. viminalis* from the late Kinderhookian (Tournaisian, late Hastarian (Tn2)) and *A. rupinus* from the early Osagean (Tournaisian, Ivorian (Tn3a-Tn3c)). The oldest European species are from the Ivorian (=early Osagean), where two species occur, *A. crassus* (Austin and Austin, 1843) and *A. granulatus* (Austin and Austin, 1843). By the middle Osagean, *Amphoracrinus* was extinct in North America, but during this time in Europe (Tournaisian, early Chadian (Tn3c)), *Amphoracrinus* underwent a substantial radiation. The genus also occurs in China and northern Africa but never reappeared in North America. The youngest occurrence of *Amphoracrinus* is from the Visean (Asbian, V3b Asbian = late Meramecian).

All four of the oldest *Amphoracrinus* species are relatively small compared to the younger congeners. These four species can be distinguished because *A. viminalis* has convex calyx plates; basal circlet a flat cone, visible in lateral view; radial plate approximately 1.5 times wider than high; first primibrachial a little smaller than both the radial and primaxil; and 10 free arms. *Amphoracrinus rupinus* has convex calyx plates; basal circlet a flat cone, barely visible in lateral view; radial plate approximately twice as wide as high; first primibrachial smaller than radial plate and approximately the same size as the primaxil; and 10 free arms. *Amphoracrinus crassus* has very convex calyx plates with convexity beginning approximately 0.4 mm from plate boundaries; basal circlet a flat disc, barely visible in lateral view; radial plate approximately 2.0 times wider than high; first primibrachial a little smaller than both the radial and primaxil; and 15 free arms. *Amphoracrinus granulatus* has gently convex calyx plates with varying sculpturing; basal circlet a medium cone, visible in lateral view; radial plate approximately 1.25 times wider than high; first primibrachial much smaller than the radial and much larger than the primaxil; and 20 free arms.

Initially, little was known about the anal plate series of this species. Hall and Whitfield (1875, p. 165) wrote "The first anal is smaller than the first radial, and above they have not been determined." A more complete description was given by Wachsmuth and Springer (1897, p. 591), who reported two or three plates follow the primanal. However, the condition with three anals above the primanal was considered abnormal. Material for this study includes one specimen (CMCIP 46093b) that has three plates above the primanal. However, in this example the right lateral plate rather than the center plate was smaller than the others. The two-plate condition is considered normal (Fig. 3.1).

Arm branching is highly variable in this species. Figure 4 illustrates this variability, both within rays and among rays (also note Figs. 2.1, 2.3, 2.4, 3.2).

Measurements.—See Table 1.

Genus ARYBALLOCRINUS Breimer, 1962

Type species.—Actinocrinus (Megistocrinus) whitei Hall, 1861.

ARYBALLOCRINUS MARTINI new species
Figure 5.1, 5.5

Diagnosis.—Calyx interpreted as medium globe shape; approximately as high as wide, maximum width at approximately first secundibrachial; calyx plates smooth, except for median ray ridges low in calyx beginning on radial plate, (presence or absence of median anitaxial ridge unknown); radial plates 1.2 times higher than wide; (interradial areas unknown), primaxils pentagonal.

Description.—Calyx large, medium globe shape; as wide as high; maximum width approximately at level of first secundibrachial, arms grouped; calyx plates very thin, high, smooth sculpturing in all plates low in calyx; median ray ridges begin on radial plate, extends onto second primibrachial but not onto first tertibrachial. Basal circlet truncate proximally (Fig. 5.5), high, visible in side view; basal concavity shallow; other aspects unknown. Radial plates presumably five, hexagonal or heptagonal, 1.2 times higher than wide, smooth (except for median ray ridge) (Fig. 5.5). Regular interrays, CD interray, and tegmen unknown. First primibrachial hexagonal,

TABLE 1—Measurements for *Amphoracrinus viminalis* (in mm, * incomplete or specimen compacted, ** holotype).

Specimen	Crown height	Calyx height	Calyx width	Basal plate height	Basal circlet width	Radial plate height	Radial plate width	Primaxil height	Primaxil width
NYSM 6117**	—	—	—	1.5	4.8	3.1	5.5	2.1	3.4
CMCIP 46093b	40.7	6.7	12.4	1.3	3.9	2.8	4.4	1.9	3.0
CMCIP 46130	42.2	7.2	15.3	1.3	4.5	2.8	4.3	1.9	4.1
CMCIP 46131	52.8	7.8	17.0	1.2	4.0	3.0	4.3	1.8	2.8
CMCIP 46132	46.7	8.4	18.5	1.2	5.0	3.5	5.3	1.9	3.2
CMCIP 46133	51.2	7.2	21.9	1.2	4.7	3.1	4.5	1.9	3.0
CMCIP 46134	39.5	5.5	12.3	0.8	3.2	2.5	3.6	1.7	2.8
CMCIP 46135	54.3	8.3	17.2	1.2	4.0	3.1	5.1	1.9	3.1

approximately as high as wide, much smaller than radial plates but larger than primaxil (Fig. 5.5); number of primibrachials unknown; primaxil in sutural contact above with only the first secundibrachial fixed in calyx; median ray ridge does not continue onto secundibrachials; first secundibrachial in sutural contact with adjacent first secundibrachial medially; second secundibrachial all or partially in calyx, beginning of free arms; first and second secundibrachial uniserial. Probably one or two intrabrachial plates between adjacent half rays at level of secundibrachials. Other aspects of calyx unknown.

Free arms 10, begin on third secundibrachial, narrow, aborally convex, branching isotomously at least two times for at least 20 total arms (Fig. 5.1). Free arm brachials biserial, aboral sutures straight. Column circular, latera convex with ridge around circumference. Heteromorphic proximally, nudinodals separated by one or two priminternodals; distally questionably homeomorphic.

Discussion.—Two specimens of *A. martini* n. sp. are known from the Meadville Shale. Both are very poorly preserved. However, despite the poor preservation of the holotype, a substantial number of species-diagnostic characters are preserved, allowing new species determination. Ausich and Sevastopulo (2001) listed species-diagnostic characters that are followed here. Accordingly, *A. martini* is distinct having a globe-shaped calyx that is approximately as high as wide, first primibrachial at the approximate widest level of calyx (although this is difficult to determine on the available specimens), smooth plate sculpturing, median ray ridges that begin on the radial plate, and radial plates higher than wide. *Aryballocrinus whitei* (Hall, 1861), *A. sampsoni* (Miller and Gurley, 1896), *A. awthornensis* (Wright, 1955a), and *A. eirensis* Ausich and Sevastopulo (2001) all also have globe-shaped calyxes; the level of the widest portion of the calyx, where known, at the first primibrachial; and median ray ridges. However, they are distinct because *A. martini* has smooth plate sculpturing, median ray ridges that begin on radial plates, and the radial plate higher than wide. In contrast, *A. whitei* has smooth calyx plate sculpturing, median ray ridges that begin on either the basal or radial plate, and radial plate wider than high; *A. sampsoni* has smooth calyx plate sculpturing, median ray ridges that begin on the basal plates, and the radial plate wider than high; *A. awthornensis* has stellate calyx plate sculpturing, median ray ridges begin on basal plates, and radial plates as high as wide; and *A. eirensis* has smooth calyx plate sculpturing, median ray ridges begin on the first primibrachial, and radial plates are wider than high.

Poor preservation and few specimens per species is very typical for *Aryballocrinus* because this genus has a relatively large, ellipsoidal to globe-shaped calyx that is comprised of very thin plates. Thus, it is highly susceptible to compaction and disarticulation.

Etymology.—This new crinoid recognizes Jerry Martin, for generously providing land access for crinoid collection for the Richfield, Ohio portion of the specimens represented in this study.

Material examined.—Holotype CMNH 5802; CMNH 5931 questionably assigned to this species.

Occurrence.—*Aryballocrinus martini* from the Meadville Shale Member of the Cuyahoga Formation at Lodi in northeastern Ohio.

Measurements.—CMNH 5082, holotype, crown height, 61.0*; calyx height, 32.7*; radial plate height, 10.8; radial plate width, 5.8. CMNH 5931, crown, 63.2*; calyx height, 30.6*; calyx width, 41.5*; column height, 78.1*; nodal width, 11.1.

Family COELOCRINIDAE Bather, 1899
Genus AOROCRINUS Wachsmuth and Springer, 1897

Type species.—*Dorycrinus immaturus* Wachsmuth and Springer in Miller, 1889.

AOROCRINUS HELICE (Hall, 1863)
Figures 6.1–6.8, 7.1, 7.4–7.6

Actinocrinus helice HALL, 1863, p. 53; HALL, 1864, p. 53; SHUMARD, 1868, p. 350; HALL AND WHITFIELD, 1875, p. 163, pl. 11, figs. 5–8; WACHSMUTH AND SPRINGER in MILLER, 1889, p. 22.

Aorocrinus helice (HALL, 1863). WACHSMUTH AND SPRINGER, 1897, p. 481, pl. 45, figs. 2 and questionably 5; WELLER, 1898, p. 90; BASSLER AND MOODEY, 1943, p. 305; AUSICH, 1996, p. 249, fig. 17-7.5; WEBSTER, 2003.

Agaricocrinus helice (HALL, 1863). MILLER, 1897, p. 732; WELLER, 1898, p. 70.

Actinocrinus helice var. *eris* HALL, 1863, p. 53; HALL, 1867, p. 53; WELLER, 1898, p. 90; BASSLER AND MOODEY, 1943, p. 305.

Actinocrinus eris HALL, 1863. HALL AND WHITFIELD, 1875, p. 164, pl. 11, figs. 9, 10; WELLER, 1898, p. 90; BASSLER AND MOODEY, 1943, p. 305.

Agaricocrinus eris (HALL, 1863). MILLER, 1889, p. 220; MILLER, 1897, p. 732.

Diagnosis.—Calyx low cone shape, slightly lobate at arm openings, calyx plates with moderate to highly nodose sculpturing, deeply impressed sutures, two ranges of interradial plates fixed into calyx, CD interray with two ranges of plates fixed above the primanal, tegmen not known, two to four arms per ray.

Description.—Calyx small in size; truncate low cone shape (Fig. 6.1); calyx plate sculpturing variable, central protuberance formed by moderate (Fig. 6.5) to strong (Fig. 6.6) node, poorly to well-developed radiating ridges forming depressed plate corners (Fig. 6.7), sutures deeply impressed, rays may be emphasized with nodes or poorly developed ray ridge; arms slightly grouped (Fig. 6.4, 6.7); may have few ridges crossing

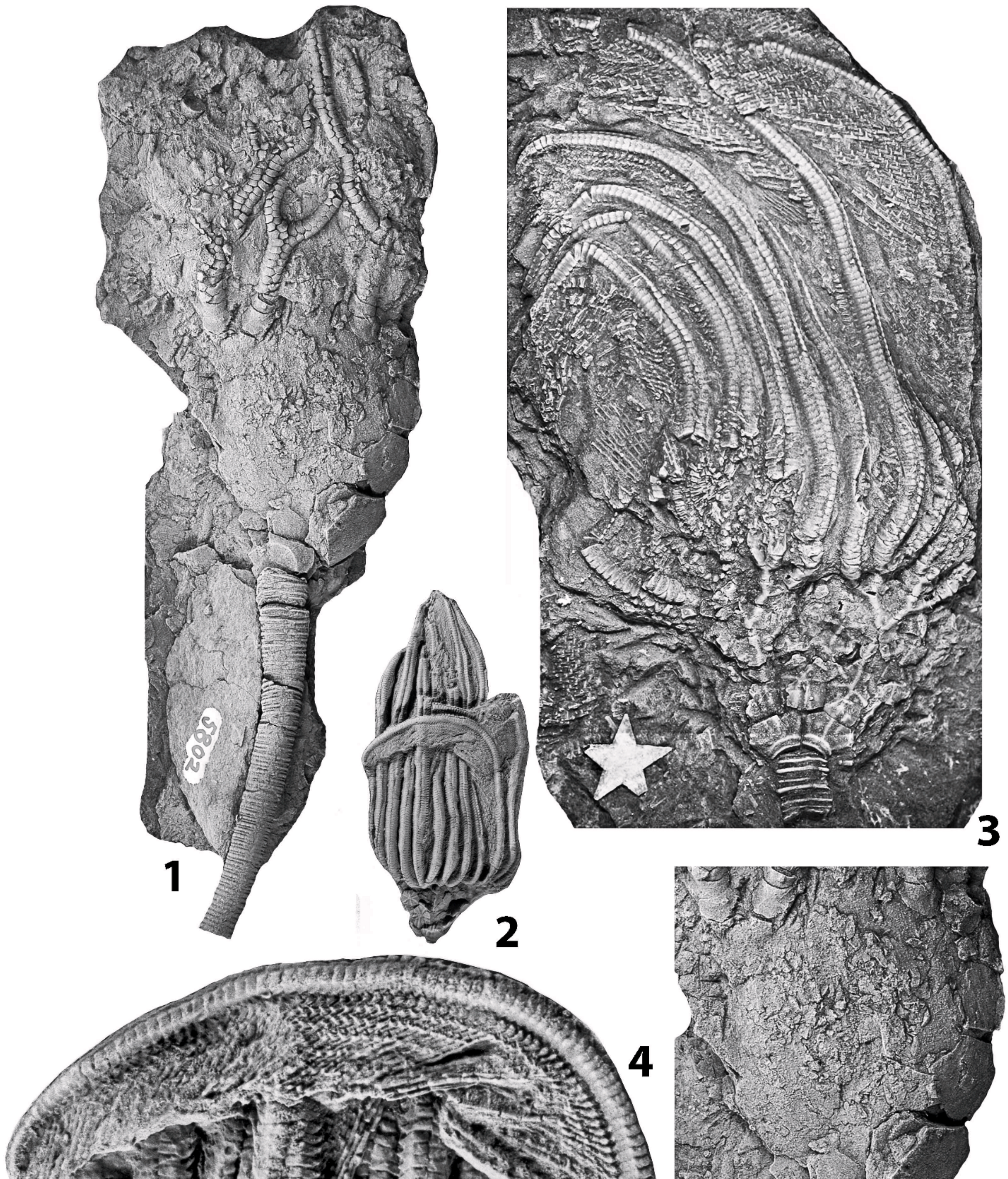

FIGURE 5—*Aryballocrinus martini*, n. sp. and *Cusacrinus daphne* (Hall, 1863b). *1*, *5*, *A. martini*, lateral view of crown, holotype, CMNH 5802; *1*, ×1.5; 5, ×2.0; *2, 3, 4, C. daphne,* CMCIP 46106: *2*, lateral view of crown, ×1.0; *3*, lateral view of crown, holotype, NYSM 6115 (previously illustrated in Hall and Whitfield, 1875, pl. 11, fig. 11), ×2.0; *4*, details of arm and pinnules, ×4.0.

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sutures to adjoining plates. Basal circlet very low (Figs. 6.3, 7.5), truncate proximally, may not be visible in lateral view with basal circlet hidden by nodose radial plates or visible in lateral view; where visible, approximately 30 percent of calyx height, shallow basal concavity formed by nodose basals and/or nodose radial plates; three equal basal plates, wider than high (mean height to width ratio, 0.35) either nodose and elongate laterally projecting node dominating plate or elongate proximally projecting node dominating plate. Radial circlet approximately 20 percent of calyx height; radial plates five, hexagonal (A, C, and D rays) or heptagonal (B and E rays), mean height-width ratio 0.65 depending on whether in contact below with one or two basal plates, wider than high, moderately to strongly nodose. Regular interrays in relatively narrow contact with tegmen (Fig. 7.1, 7.6), all plates either nodose or smooth; first interradial commonly octagonal, varies from hexagonal to 11-sided, approximately as high as wide or wider than high, smaller than radial plates and larger than first primibrachials. Second range typically with two plates but may have one or three. First interradial in lateral contact with first primibrachial, second primibrachial and first secundibrachial; rarely first secundibrachial not in sutural contact with first interradial. In interrays, sutures between ray and interradial plate series along relatively narrow depression lacking ridges connecting nodes from plate to plate or with one coarse ridge crossing sutures. Interradial plating fixed in calyx typically 1-2, rarely 1-1 or 1-3 (Fig. 7.1). Primanal heptagonal (Figs. 6.2, 6.3, 7.1), approximately as high as wide, height to width ratio approximately 1.06, larger that radials, convex to nodose, with coarse ridges connecting central node to that of adjacent plates, interrupts radial circlet; plating in CD interray P-3.

Fixed brachials nodose to very nodose, forming broad ray ridges from convexity of plates (Fig. 6.8). First primibrachial wider than high (height to width ratio approximately 0.52), much smaller than radial plates, approximately same size or slightly smaller than primaxil; second primibrachial axillary, pentagonal. First or second secundibrachial fixed in calyx, first secundibrachial may be axillary with one or two tertibrachials fixed in calyx.

Tegmen not visible on available specimens, one large plate immediately above primanal that appears to be beginning of anitaxis, other proximal tegmen plates very small. Two (Fig. 6.5), three (Fig. 6.3), or four free arms (Fig. 6.7) per ray; unbranched, for a total of 12 to 18 arms. First free brachial typically uniserial then biserial. Distal brachials either flattened or convex. If distal brachials flattened somewhat aborally, arms curve abaxially to form somewhat flattened distal-most crown; if brachials convex, distal arms taper, incurved (Fig. 6.8).

Column circular, holomeric, heteromorphic with N212 noditaxis; strongly convex latus (Figs. 6.1, 7.6).

Material examined.—Lectotype of *A. helice* NYSM 6119; paralectotype NYSM 6120, both from Richfield, as is NYSM 6118, the holotype of *A. helice* var. *eris* Hall (1863), a junior synonym of *A. helice.* Other Richfield specimens (some specimen numbers with multiple individuals): CMCIP 46055–46097, 46100, 46101, 46112, and 46114. Lodi specimens: CMNH 4777, 5586–5592, 5673, 5681, 5683, 5685, 5687, 5689, 5747–5751, 5801, 5808, 5820, 5821, 5823, 5829, 5856, 5880, 5905 to 5908, 5919 to 5926, 5932, 5939, 5949–5952, 5954, 5956, 5979, 5982, 5987, 6800, 9021, 9025–9027, 9032, 12143, 12151, 12154–12156, 12167, 12195, 12203, 12236, 12258–12260, 12263, 12266, 12268–12278, 12282, 12283, 12285–12288, 12375, 13419, and 13420.

Occurrence.—*Aorocrinus helice* from the Meadville Shale Member of the Cuyahoga Formation at Lodi and Richfield in northeastern Ohio.

Discussion.—*Aorocrinus helice* was described in 1863; however, it was not illustrated until Hall and Whitfield (1875, pl. 11, figs. 5–8). They illustrated two specimens: NYSM 6119, (Hall and Whitfield, 1875, pl. 11, figs. 5, 6) and NYSM 6120, (Hall and Whitfield, 1875, pl. 11, figs. 7, 8) (Fig. 6.1 and 6.2, respectively). The diagnostic calyx shape and calyx plate sculpturing is better preserved on NYSM 6119. Thus, NYSM 6119 is designated the lectotype, and NYSM 6120 is the paralectotype.

The two species of *Aorocrinus* from the Cuyahoga Formation are distinguished by distinctive calyx shapes and calyx plate sculpturing. *Aorocrinus helice* has a low, cone-shaped calyx and moderately to highly nodose calyx plates with sutures deeply impressed. In contrast, *A. meyeri* n. sp. has a low bowl-shaped calyx and relatively thin calyx plates with multiple thin to coarse ridges connecting to adjacent plates. *Aorocrinus* specimens can be recognized by the distally expanded arms that enroll inward distally. However, the calyx is required to distinguish between the two species based on the characters mentioned above.

Most species of *Aorocrinus* have smooth calyx plate sculpturing with low calyx plate convexity. The moderate to highly convex calyx plates in *A. helice* are unique. Also the calyx profiles of most species are not as low as they can be on specimens of *A. helice*.

Arm number and calyx plate sculpturing are variable in *A. helice*. Arm number ranges from 12 to 18, with 16 most common. Figure 8 illustrates arm number variability among rays. With minor exception, this plot verifies Hall and Whitfield's (1875, p. 163) original observations: "A constant feature of this species, so far as observed, is the existence of two arms in the anterior ray, and four in each of the postero-lateral rays, while in the antero-lateral divisions there may be two, three, or four arms in one or both rays." Hall and Whitfield (1875, p. 164) described *Actinocrinus eris* and Wachsmuth and Springer correctly recognized this species as a junior synonym of *A. helice*. Calyx plates are not strongly nodose on this junior synonym, and it has only three arms in the C and D rays. The *eris* variant is rare with only two specimens known with three arms in both the C and D rays. These two specimens also have a less nodose plate sculpturing (holotype, Fig. 6.3).

The single most common feature with variation is calyx plate sculpturing. Calyx sculpturing in *A. helice* ranges from specimens with broadly convex plates lacking ridges, to those with strongly nodose plates, to nodose plates with short radiating ridges.

The tegmen was not visible on any specimens of *A. helice* available for study. However, Wachsmuth and Springer (1897, p. 481, pl. 45, fig. 5) questionably identified a specimen that had one, distally projecting spine from the center of the tegmen.

Four specimens assigned to *A. helice* (Hall) preserve arm regeneration. One arm in the A ray of CMCIP 46057 (Fig. 6.4) and one in the D ray of CMCIP 46081B have the distal portion of the arm regenerating. Two entire arms of the C ray in CMCIP 46081B and five adjacent arms in the C ray of CMCIP 46089 are smaller than the other arms. CMNH 5824 is an unusual specimen of *A. helice* because it has the distal arms divided on all visible half-rays. This is interpreted as a record of arm regeneration. Alternatively, this could be a

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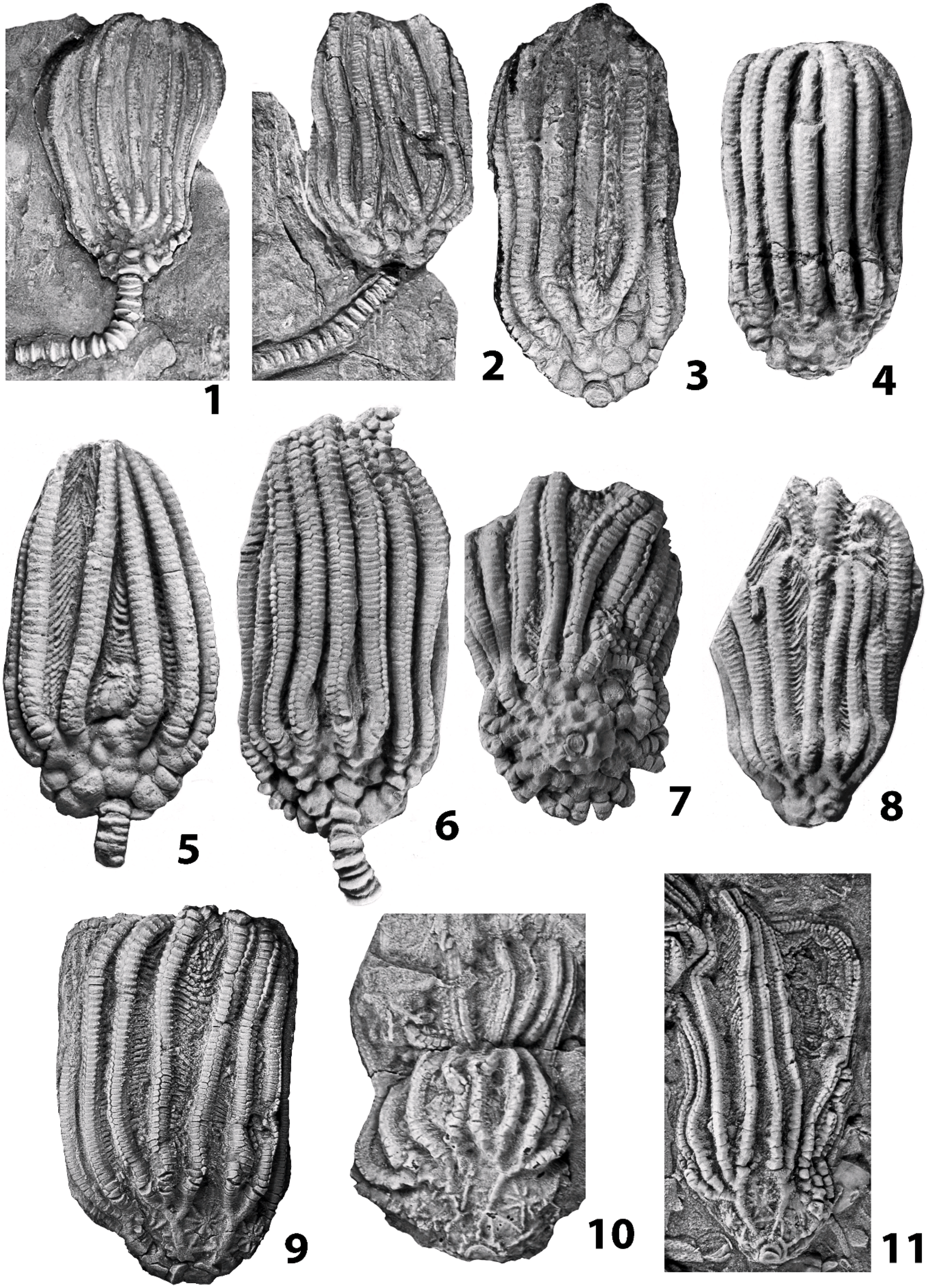

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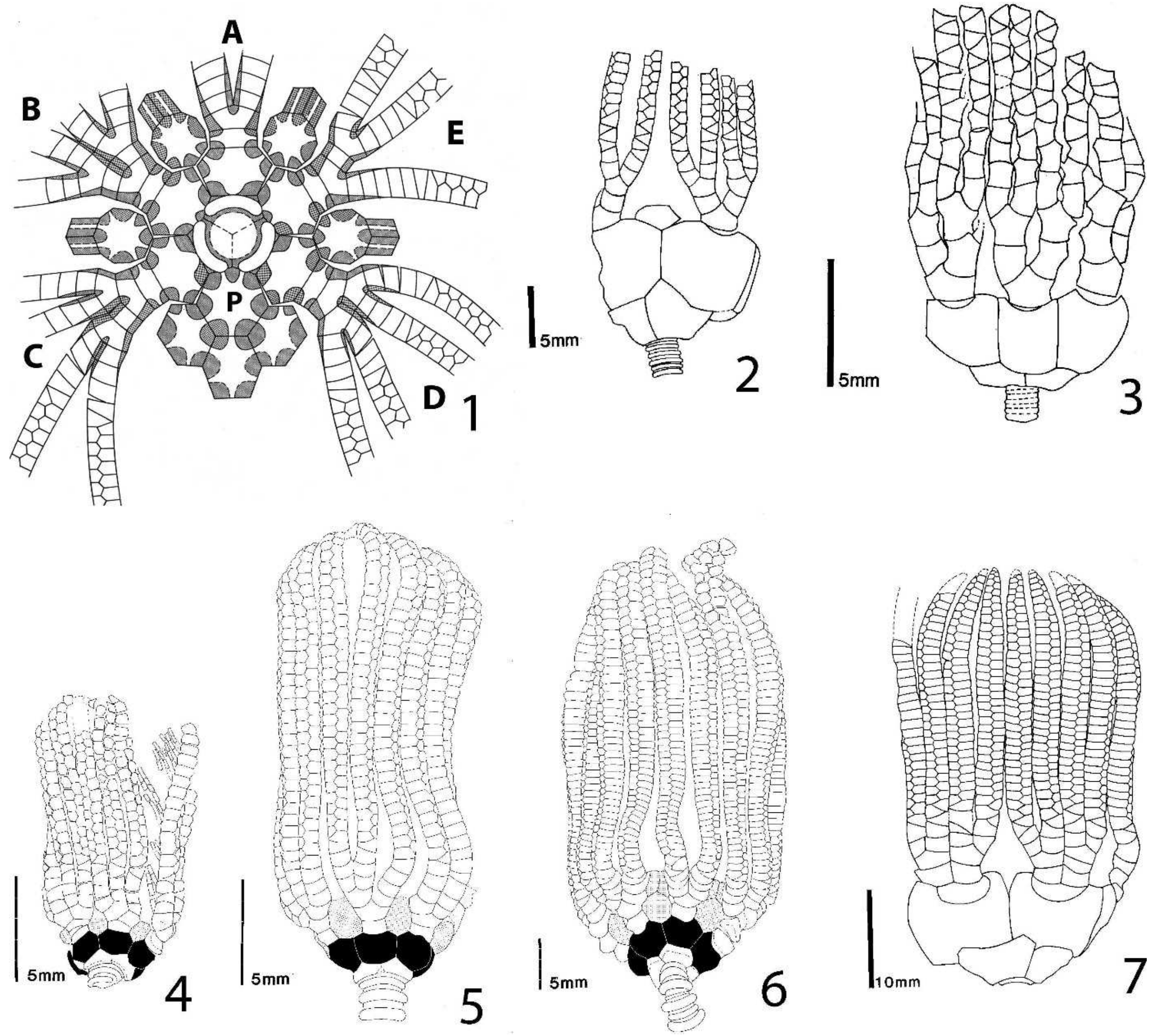

FIGURE 7—*Aorocrinus helice* (Hall, 1863b), *Platycrinites* s.l. *graphicus* (Hall, 1863b), and *Platycrinites* s.l. *lodensis* (Hall and Whitfield, 1875). *1*, *4–6*, *A. helice*: *1*, plate diagram (A–E ray designations, P. indicates primanal, gray indicates depressions on calyx); *4–6*, (black, radial plates; scales as indicated); *4*, CMCIP 46059; *5*, CMCIP 46061D; *6*, CMCIP 46055; *2*, *3*, *P.* s.l. *graphicus*; (scales as indicated): *2*, CMCIP 46146; *3*, CMCIP 46149a (compare to *Fig. 8.3*) neotype, CMCIP 46143; *7*, *P.* s.l. *lodensis*, CMCIP 46143. (Scales as indicated).

specimen of a different taxon, but the former is considered more probable.

Sixteen specimens are complete enough to measure for the analysis of growth in *A. helice*. These specimens range in size from a calyx height and width of 4.8 and 8.5 mm to 9.1 and 15.5 mm (Table 2). Examples of this size range are Figure 4.4–4.6. The growth rate of the calyx height is greater than the calyx width; but like most other comparisons for *A. helice*, the change is not allometric (Table 3; Fig. 1, Supplementary data archive, www.journalofpaleontology.org). The only components of growth on *A. helice* that approaches allometry are the calyx width versus the radial plate width and the primaxil height versus the primaxil width (Table 3; Figs. 1–10, Supplementary data archive). The positive allometry of the primaxil width increasing more rapidly than primaxil height is similar to results on Ordovician crinoids (e.g., Brower, 2002).

←

FIGURE 6—*Aorocrinus* from the Cuyahoga Formation. *1–8, A. helice* (1863b): *1*, lateral view of crown, lectotype, NYSM 6119 (previously illustrated in Hall and Whitfield, 1875, pl. 11, fig. 6), ×1.5; *2*, CD-interray view of crown, paralectotype, NYSM 6120 (previously illustrated in Hall and Whitfield, 1875, pl. 11, fig. 8), ×1.5; *3*, D-ray lateral view of crown, holotype of *A. helice* var. *eris* Hall and Whitfield, 1875, NYSM 6118 (previously illustrated in Hall and Whitfield, 1875, pl. 11, fig. 9), ×1.75; *4*, A-ray lateral view of crown with regenerating arm, CMCIP 46057, ×2.0; *5*, lateral view of crown, CMCIP 46063, ×2.0; *6*, lateral view of crown, CMCIP 46055, ×2.0; *7*, basal view of calyx with arms, CMCIP, 46062, ×2.0; *8*, lateral view of crown, CMCIP 46098, ×2.0; *9–11, A. meyeri* n. sp.: *9*, B-ray lateral view of crown, holotype, CMCIP 46098, ×2.0; *10*, lateral view of crown, paratype CMNH 5929, ×2.0; *11*, lateral view of crown, paratype, CMNH 5951a, ×2.0.

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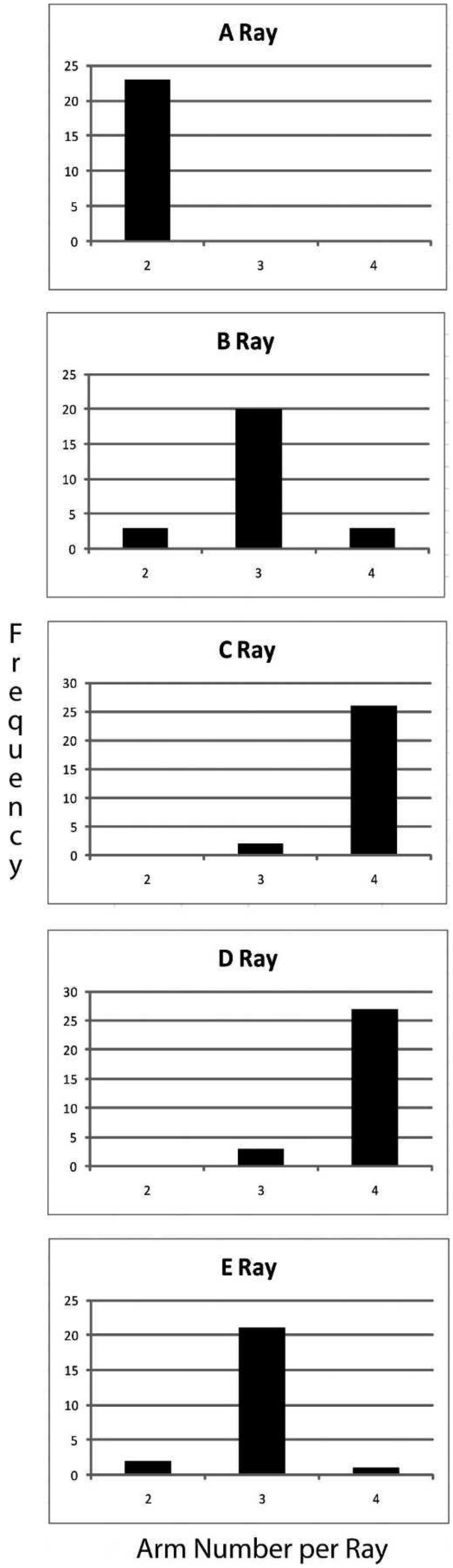

FIGURE 8—Histograms indicating frequency of free arm number per ray among 47 specimens of *Aorocrinus helice* in the CMCIP collections.

Although only one measure is considered, the arms appear to have grown allometrically, whereas the calyx largely did not.

Measurments.—See Table 2.

AOROCRINUS MEYERI new species
Figure 6.9–6.11

Diagnosis.—Calyx low bowl to low cone shape, slightly lobate at arm openings, calyx plates with single ridge stellate sculpturing connecting to adjacent plates, two ranges of interradial plates fixed into calyx, CD with one range of plates fixed above primanal, tegmen not known, two to four arms per ray.

Description.—Calyx small; low bowl to truncate low cone shape, (Fig. 6.9); calyx plates relatively thin; arms grouped; ray ridges; calyx plates with typically one thin to coarse ridge connecting to adjacent plates (Fig. 6.11). Basal circlet truncate proximally, visible in side view, very low, approximately 13 percent of calyx height, shallow basal concavity formed in basal plates; basal plates three, equal in size, low elongate proximal nodes at base of calyx. Radial circlet approximately 30 percent of calyx height; radial plates five, hexagonal or heptagonal, depending on whether one or two basal plates beneath, wider than high, centrally convex with coarse ridges connecting from central concavity to all adjacent plates. Regular interrays in relatively broad contact with tegmen; first interradial decagonal, approximately as high as wide, flat with narrow ridges from flattened central region to all adjoining plates (Fig. 6.9), approximately same size as radials and larger than first primibrachial. Second range with four plates, fixed plating 1–4. First interradial plate in contact with first and second primibrachial and first secundibrachial. Sutures between ray and interradial plates along a wide region with interradial plates flat; narrow ridges connecting first interradial to all adjacent plates. Primanal heptagonal, approximately as high as wide, sculpturing same as radial plates, interrupts the radial circlet; fixed plating in the CD interray P-3. Fixed brachials form distinct ray ridges. First primibrachial wider than high, smaller than radial plates and approximately same size as primaxil, tetragonal; second primibrachial axillary, pentagonal. Three to five fixed tetragonal secundibrachials or first secundibrachial axillary with two or three fixed tertibrachials.

Tegmen not known.

Two, three (Fig. 6.9), or four free (Fig. 6.10) arms per ray, unbranched. First few fixed brachials tetragonal, then with biserial, aborally rounded, with distal brachials convex to slightly nodose. Distal arms flattened somewhat aborally and curve adaxially to form a somewhat flattened distal crown.

Column circular, proximally latera very convex on nodals with single low, flat internodal. Distally, priminternodals become high and latera very convex. Internodals grow in height and convexity of latera with N3231323 noditaxis, most developed column preserved. Columnal facet and holdfast unknown.

Etymology.—This species name recognizes David L. Meyer for his significant contributions to our understanding of crinoids and his encouragement to pursue this project.

Material examined.—*Aorocrinus meyeri* n. sp. holotype CMCIP 46098, from Richfield; paratypes CMNH 5687a; 5822a, 5822b; 5880a; 5929, and 5951a from Lodi. Additional specimens from Lodi: CMNH 5673a, 5673b and 5939.

Discussion.—*Aorocrinus meyeri* n. sp. is compared to *A. helice* in the discussion above. *A. douglassi* (Miller and Gurley, 1897) is the only other species of *Aorocrinus* with stellate calyx plate sculpturing. This species is from the Kinderhookian Lodgepole Formation of the western United States. *Aorocrinus*

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TABLE 2—Measurements for *Aorocrinus* (in mm, * incomplete or specimen compacted, ** holotype).

Specimen	Crown height	Calyx height	Calyx width	Basal plate height	Basal circlet width	Radial plate height	Radial plate width	Primaxil height	Primaxil width
Aorocrinus helice									
CMCIP 46055	40.3	9.1	15.5	1.3	3.2	2.4	3.8	1.7	2.7
CMCIP 46056	37.9	7.6	14.4	1.2	2.8	2.3	3.9	1.6	2.8
CMCIP 46057	31.6	6.4	11.7	1.1	2.8	2.0	3.3	1.1	2.8
CMCIP 46058	33.9	6.5	17.0	1.0	2.9	2.0	3.4	1.3	2.4
CMCIP 46059	16.3	6.0	5.0	0.6	1.5	1.1	1.7	0.4	1.2
CMCIP 46060	24.2	4.0	8.5	0.5	1.4	1.3	2.4	0.9	1.8
CMCIP 46061a	22.7	5.3	9.9	0.6	2.1	1.3	2.0	0.7	1.5
CMCIP 46062	22.5	5.3	10.5	1.0	2.4	1.7	2.8	2.0	2.2
CMCIP 46063	33.9	6.7	12.8	—	—	2.2	3.5	2.4	3.0
CMCIP 46064a	23.5	4.2	9.7	0.8	1.9	1.6	2.4	0.9	2.1
CMCIP 46065	33.3	6.7	16.1	—	—	1.1	3.2	1.3	2.5
CMCIP 46066	38.5	8.5	14.3	0.9	3.1	1.0	3.3	1.4	2.8
CMCIP 46067	—	6.5	13.0	0.7	2.6	1.3	3.4	1.2	2.8
CMCIP 46068	31.5	5.5	14.2	0.8	2.0	1.1	2.8	1.2	2.0
CMCIP 46069	31.1	6.8	13.4	—	—	1.8	2.6	1.1	2.0
CMCIP 46070	29.8	7.8	11.8	1.1	2.9	1.9	2.5	1.3	2.2
CMCIP 46071	27.6	5.3	13.0	0.6	1.8	1.7	2.9	1.2	2.3
CMCIP 46072	30.9	5.3	10.8	0.7	2.3	1.0	2.7	1.2	2.0
CMCIP 46073	29.6	5.6	11.5	0.6	1.8	1.2	2.7	1.2	2.1
CMCIP 46074	24.2	4.5	9.4	0.7	2.2	1.6	2.4	0.8	1.6
CMNH 5689	36.1	5.4	12.8	1.1	4.0	2.6	3.5	—	—
Aorocrinus meyeri n. sp.									
CMCIP 46098**	35.1*	8.2	13.5	1.2	—	2.3	3.5	1.4	2.7
CMNH 5929	33.5	8.4	10.8	1.4	3.4	3.2	3.2	1.8	2.2

douglassi Miller and Gurley (1897, pl. 2, fig. 26) (CMCIP 5929), is very similar to the Cuyahoga Formation species. However, *A. meyeri* has smaller first primibrachials, stellate sculpturing on ray plates with a single ridge connecting to adjacent plates; and two to four free arms per ray. In contrast, *A. douglassi* has a larger first interradial plate, stellate sculpturing with one, two, or more ridges connecting to adjacent plates; and six free arms.

Occurrence.—*Aorocrinus meyeri* from the Meadville Shale Member of the Cuyahoga Formation in northeastern Ohio from Lodi and Richfield.

Measurements.—See Table 2.

Family ACTINOCRINITIDAE Austin and Austin, 1842
Subfamily CACTOCRININAE Ubaghs, 1978b
Genus CUSACRINUS Bowsher, 1955

Type species.—*Actinocrinus nodobrachiatus* Wachsmuth and Springer, 1889.

CUSACRINUS DAPHNE (Hall, 1863)
Figures 2.4, 5.2–5.4, 9.2, 9.3, 9.8, 9.9

Actinocrinus daphne HALL, 1863, p. 52; HALL 1864, p. 52; SHUMARD, 1868, p. 350; HALL AND WHITFIELD, 1875, p. 162, pl. 11, fig. 11; WACHSMUTH AND SPRINGER in MILLER, 1889, p. 217; MILLER, 1897, p. 731; WACHSMUTH AND SPRINGER, 1897, p. 574, pl. 56, fig. 1; WELLER, 1898, p. 57; BASSLER AND MOODEY, 1943, p. 269; BOWSHER, 1955, p. 12; WEBSTER, 1973, p. 93.

Actinocrinites daphne (HALL, 1863). BASSLER AND MOODEY, 1943, p. 269.

Cusacrinus daphne (HALL, 1863). BOWSHER, 1955, p. 12; WEBSTER, 1973, p. 93; WEBSTER, 2003.

TABLE 3—Statistics from consideration of allometry in *Aorocrinus helice*. H=height; W=width; BP=basal plate; BC=basal circlet; RP=radial plate; Pr1=first primibrachial. Shaded regions indicate allometry.

LogXLog	Slope	Y-intercept	r 2	p(a=1)
Calyx H vs. Calyx W	1.21	0.12	0.25	0.46
Calyx H vs. BP H	1.22	−1.03	0.53	0.34
Calyx H vs. RP H	1.21	−0.08	0.11	0.50
Calyx H vs. Pr1 H	1.6	−1.19	0.19	0.14
Calyx W vs. BP W	0.88	−0.57	0.50	0.48
Calyx W vs. RP W	0.76	−0.36	0.76	0.03
Calyx W vs. Pr1 W	0.82	−0.54	0.69	0.17
BP H vs. BP W	0.87	0.43	0.79	0.26
RP H vs. RP W	0.76	0.30	0.13	0.18
Pr1 vs. Pr2	0.62	0.29	0.71	<0.01

Diagnosis.—Radial circlet relatively low; sculpturing multi-stellate; distinct median ray ridges; regular interrays in contact with tegmen; posterior interray in relatively wide contact with tegmen; and 30 free arms.

Description.—Crown large, arms three or more times higher than calyx (Figs. 5.3, 9.9). Calyx medium; low cone shape; cup plates relatively thin; arms not grouped; calyx plates with irregular stellate sculpturing, with one or more ridges connected to ridges of adjacent plates (Fig. 9.3, 9.8). Basal circlet truncate proximally, visible in side view, relatively low, approximately 20 percent of calyx height (Fig. 3.4); basal plates three, unequal in size, wider than high, stellate sculpturing as described above, may have a low ridge around proximal-most portion of basal circlet. Radial circlet approximately 30 percent of calyx height; radial plates five, hexagonal (A, C, and D rays) or heptagonal (B and E rays) typically wider than high.

Regular interrays in relatively narrow contact with tegmen; first interradial hexagonal, approximately as high as wide, smaller than radials and approximately equal in size with first primibrachial. Second range typically with two plates; plating 1-2-3-2-1. Primanal hexagonal, higher than wide, smooth, somewhat smaller than radial plates, interrupts the radial circlet; plating in CD interray P-2-3-5-4. Ridges define the fixed rays. First primibrachial approximately 1.5 times wider than high, much smaller than radial plates and approximately same size as primaxil, hexagonal; second primibrachial axillary, heptagonal wider than high. First secundibrachial axillary, wider than high; abaxial tertibrachitaxis unbranched, adaxial tertibrachial axillary; secundibrachtaxis or tertibrachitaxis highest plate in calyx before free arms. No fixed intrabrachial plates between adjacent half rays.

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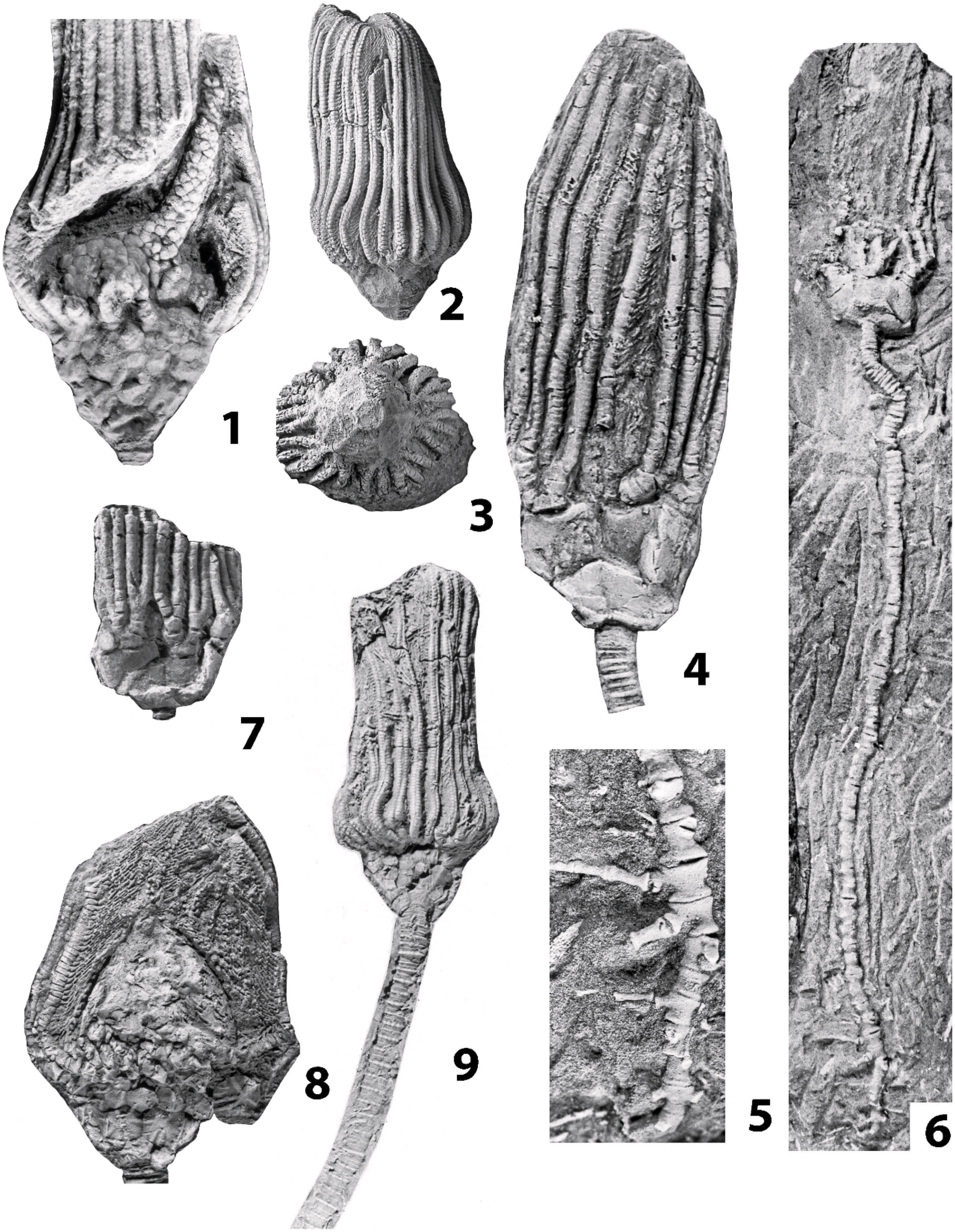

FIGURE 9—*Cusacrinus daphne* (Hall, 1863b) and *Platycrinites* s.1. *graphicus* (Hall, 1863b). *1–3, 8, 9, C. daphne: 1*, C-ray view of crown illustrating partial tegmen and anal tube, (Compare to *Fig. 2.4*), CMCIP 46108, ×2.0; *2*, C-ray lateral view of crown, CMCIP46143, ×1.25; 3, basal view of calyx illustrating distinct ray ridges and other ridges on calyx plates, CMCIP 46104, ×1.5; *8*, lateral view of crown illustrating convex-sided tegmen, CMCIP 46111, ×1.5; *9*, lateral view of crown with column attached, CMCIP 46121, ×1.0; *4–7*, *P.* s.l. *graphicus*: *4*, lateral view of crown, ×1.5; *4*, holotype, NYSM 6135 (previously illustrated in Hall and Whitfield, 1875, pl. 11, fig. 2), ×1.5; *5, 6,* CMCIP 46147a: *5*, enlargement of holdfast, ×4.0; *6*, complete specimen, ×1.0; *7*, lateral view of crown, ×1.5, CMCIP 46136c.

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TABLE 4—Measurements for *Cusacrinus daphne* (in mm, * incomplete or specimen compacted, **holotype).

Specimen	Crown height	Calyx height	Calyx width	Basal plate height	Basal circlet width	Radial plate height	Radial plate width	Primaxil height	Primaxil width
NYSM 6115	79.5	18.5		3.0	5.1	4.1	4.0	2.9	4.0
CMCIP 46103	60.6	11.6		2.6	5.3	5.1	5.4	2.4	3.4
CMCIP 46104	43.9	8.1	—	—	—	—	—	—	—
CMCIP 46105a	36.0	6.8		1.2	3.1	2.2	3.4	1.6	2.3
CMCIP 46105b	—	—		1.1	3.9	2.3	3.3	1.7	2.4
CMCIP 46106a	94.9	16.6		3.6	7.0	6.6	7.4	2.8	3.8
CMCIP 46107	37.8	8.4		1.1	3.7	2.9	3.8	2.0	2.9
CMCIP 46108	59.3	10.0		2.5	4.5	3.5	4.2	2.1	2.8
CMCIP 46109	—	10.3		1.6	4.5	3.6	4.9	2.1	3.0
CMCIP 46110	44.0	7.9		1.7	3.7	3.2	3.8	1.8	3.0
CMCIP 46111	—	10.0		2.3	5.8	4.4	5.4	—	—
CMCIP 46112a	26.0	4.0		1.0	2.2	1.9	2.9	1.3	2.2
CMCIP 46112b	32.6	7.7	—	—	—	—	—	—	—
CMCIP 46113a	53.7	10.0		1.7	—	3.9	3.7	2.4	3.2
CMCIP 46115	65.1	13.1	—	—	—	—	—	—	—
CMCIP 46117	84.5	12.5	—	—	—	—	—	—	—

Tegmen not as high as calyx; inverted low-bowl shape (Fig. 9.1) from arm openings to base of anal tube, interradial areas depressed abaxially; plates small, convex; anal tube long, eccentric (Figs. 3.4, 9.1), shorter than arms, composed of small, convex plates.

Free arms 25 to 30, unbranched (Fig. 9.2). Proximal tertibrachials or quartibrachials cuneate uniserial then biserial distally, aborally rounded. Pinnules long (Fig. 5.2); oriented obliquely, held together as cohesive unit by short spines along distal margin that overlaps adjacent pinnular (Fig. 5.4); distal arm tips nonpinnulate and recurve inward with arms closed.

Column circular subpentagonal, heteromorphic, latera convex with nodals most convex and successive cycles less convex (Fig. 9.9). Noditaxis N212 proximally.

Material examined.—Holotype of *C. daphne* NYSM 6115 from Richfield. Additional material from Richfield: CMCIP 46103; 46104; 464106a–46108; 46110; 46111; 46113a; 46115; 46119a, 46119b; and 46121a. Specimens from Lodi: 5212; 5674; 5677; 5825a, 5825b; 5948; 9506; 9508; 9513a; 9518; 9519; 12146; 12153; 12258c; 12260a; 12266; 12279; and 12280. CMNH 12289 and 12294 questionably assigned to *C. daphne*.

Occurrence.—*Cusacrinus daphne* from the Meadville Shale Member of the Cuyahoga Formation at Lodi and Richfield in northeastern Ohio.

Discussion.—Again, this 1863 Hall taxon was not illustrated until Hall and Whitfield (1875, pl. 11, fig. 11). Only one specimen was illustrated, so NYSM 6115 is regarded as the holotype.

Cusacrinus is a genus with considerable morphological variability divisible into two basic morphological groupings. *C. daphne* is in the *Cusacrinus* group with a relatively low radial circlet, regular interrays in contact with the tegmen, posterior interray in contact with the tegmen, and 30 free arms. Within this group, *C. daphne* is unique with distinct medial ray ridges, multistellate calyx sculpturing, and a relatively wide connection between the posterior interray and the tegmen. The species most similar to *C. daphne* are *C. gracilis* (Wachsmuth and Springer, 1897), which lacks multistellate calyx plate sculpturing, and *C. viaticus* (White, 1874), which has a lower calyx, although this species is very poorly understood (Webster and Lane, 1987).

An interesting feature in *C. daphne* is the series of overlapping spines that hold pinnules together as cohesive paddle-like units (Fig. 5.4), which Seilacher (2011) referred to as "Velcro" attachments. This feature is also known in the closely related genus *Cactocrinus* (Wachsmuth and Springer) and in *Dialutocrinus* Wright, 1955a. Apparently, pinnules were held at a relatively constant angle to the arm axis and movement in a vertical mode was restricted. The resulting pinnular spacing may have been too dense to allow water to flow between pinnules. However, if that was the case, this unusual pinnular array could presumably have created sufficient eddying for effective feeding.

CMCIP 46104 is an unusual specimen because it has a relatively large first interradial plate that is similar to *A. meyeri*. However, the arm number and pinnules identify this crinoid with *C. daphne*. This is a smaller specimen, so these differences may be attributed to size, but this is not clear.

Growth in *C. daphne* is evaluated with six specimens that encompass a calyx height range from 4.0 to 18.5 mm (Table 4). Preservational constraints made calyx widths an unreliable measurement, so calyx height to width is not evaluated other than the qualitative observation that through ontogeny the calyx shape changed from a more bowl shape to a more cone shape. Four of the six comparisons considered for *C. daphne* can be considered to have positive allometry (Table 5; Figs. 11–16, Supplementary data archive). These include primaxil height versus calyx height, basal circlet height versus basal plate height, radial width versus radial height, and primaxil width versus primaxil height. Thus, in contrast to *A. helice*, *C. daphne* grew allometrically to a much greater extent, which is more consistent with previous studies (e.g., Brower, 2002).

Measurements.—See Table 4.

Suborder GLYPTOCRININA Moore, 1952
Superfamily PLATYCRINITOIDEA Austin and Austin, 1842
Family PLATYCRINITIDAE Austin and Austin, 1842
Genus PLATYCRINITES J. S. Miller, 1821

Type species.—The type species for *Platycrinites* s. s. is *P. laevis* Miller, 1821.

Discussion.—Ausich and Kammer (2009) redefined generic concepts in the Platycrinitidae and recognized that European genera were historically distinguished by different characters than were North American genera. Application of all relevant characters (calyx, tegmen, and arms) is needed to distinguish

TABLE 5—Statistics from consideration of allometry in *Aorocrinus helice*. H=height; W=width; BP=basal plate; BC=basal circlet; RP=radial plate; Pr1=first primibrachial. Shaded area indicates allometry.

LogXLog	Slope	Y-intercept	r^2	p(a=1)
Calyx H vs. BP H	1.01	−0.72	0.79	0.97
Calyx H vs. RP H	0.84	0.28	0.77	0.33
Calyx H vs. Pr1 H	0.68	−0.24	0.96	<0.01
BP H vs. BP W	0.72	0.41	0.85	0.05
RP H vs. RP W	0.7	0.23	0.84	0.03
Pr1 vs. Pr2	0.77	0.23	0.92	0.03

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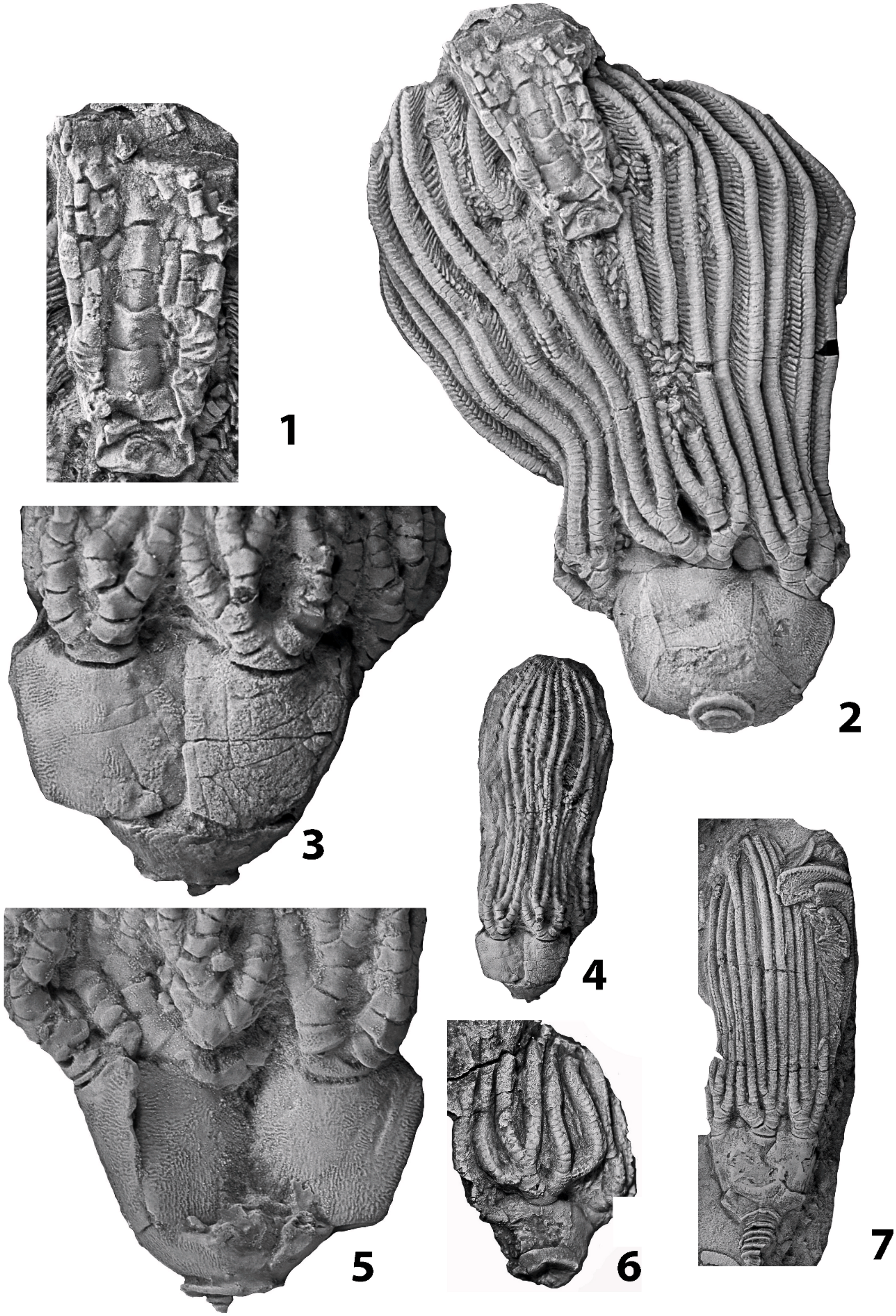

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genera in this family. However, the majority of species are known from only the calyx or the calyx and arms with the tegmen concealed. Rather than discarding species without all characters known as *nomina dubia*, Ausich and Kammer (2009) assigned these species to *Platycrinites* sensu lato.

Unfortunately, none of the figured specimens or any new specimens available for study from the Cuyahoga Formation have the tegmen uncovered. Until the morphology of the tegmen can be determined, we recommend the *Platycrinites* s.l. designation for all valid Cuyahoga species.

Five species of *Platycrinites* have been described from the Cuyahoga Formation: *P.* s.l. *contritus* (Hall, 1863), *P.* s.l. *graphicus* (Hall, 1863), *P.* s.l. *bedfordensis* (Hall and Whitfield, 1875), *P.* s.l. *lodensis* (Hall and Whitfield, 1875), and *P.* s.l. *richfieldensis* (Hall and Whitfield, 1875), the last of which is a junior synonym of *P.* s.l. *graphicus*. *Platycrinites* s.l. *bedfordensis* is designated, herein, a *nomen dubium*.

Four distinct species of *Platycrinites* s.l. are recognized in the Meadville Shale. *Platycrinites* s.l. *contritus* has smooth calyx plate sculpturing, a concave basal circlet, radial plates slightly wider than high, radial facets approximately 50 percent of distal radial plate width, and five robust free arms per ray; *P.* s.l. *graphicus* has smooth calyx plate sculpturing, a convex basal circlet, radial plates approximately 1.25 times wider than high, radial facets approximately 33 to 50 percent of distal radial plate width, and four gracile free arms per ray (rarely more); *P.* s.l. *lodensis* has smooth calyx plate sculpturing, a convex basal circlet, radial plates as high as wide, radial facets approximately 50 percent of distal radial plate width, and four robust free arms per ray; *P.* s.l. *burkei* n. sp. has calyx plate sculpturing with numerous fine irregular ridges radiating from radial facets, a convex basal circlet, radial plates higher than wide, radial facets approximately 50 percent of distal radial plate width, and six gracile free arms per ray.

PLATYCRINITES s.l. BEDFORDENSIS (Hall and Whitfield, 1875)
nomen dubium.

Platycrinus bedfordensis HALL AND WHITFIELD, 1875, p. 161, pl. 13, fig. 4. MILLER, 1889, p. 270. LESLEY, 1889, p. 686, fig. 4.
Platycrinites bedfordensis (HALL and WHITFIELD, 1875). BASSLER AND MOODEY, 1943, p. 616; WEBSTER, 2003.
Platycrinites s.l. *bedfordensis* (HALL AND WHITFIELD, 1875). AUSICH AND KAMMER, 2009, p. 704.

Material examined.—Syntypes OSU 4340.

Occurrence.—*Platycrinites bedfordensis* from the Meadville Shale Member of the Cuyahoga Formation in northeastern Ohio at Richfield.

Discussion.—The syntypes are exceedingly poorly preserved specimens. Those plates preserved are replaced by iron oxide, and the calyx or arm outer surface is clearly visible only on the distal arms. Broad proportions of the calyx plates can be estimated, but the nature of the calyx and calyx plate sculpturing cannot be ascertained. These specimens can neither be assigned to a genus with confidence nor compared to species-level taxa. Therefore, we designate this taxon a *nomen dubium*.

PLATYCRINITES s.l. CONTRITUS (Hall, 1863)
Figure 10.6

Platycrinus contritus HALL, 1863, p. 54; HALL, 1864, p. 54; SHUMARD, 1868, p. 387; HALL AND WHITFIELD, 1875, p. 166, pl. 11, fig. 4; MILLER, 1889, p. 270; LESLEY, 1889, p. 687, fig. 1; WACHSMUTH AND SPRINGER, 1897, p. 667, pl. 71, fig. 8; MILLER, 1897, p. 750; WELLER, 1898, p. 437.
Platycrinites contritus (HALL, 1863). BASSLER AND MOODEY, 1943, p. 618; WEBSTER, 2003.
Platycrinites s.l. *contritus* (HALL, 1863). AUSICH AND KAMMER, 2009, p. 704.

Diagnosis.—Calyx plate sculpturing smooth, concave basal circlet, radial plates slightly wider than high, radial facet approximately 50 percent of radial plate width, details of radial facet unknown, five robust arms per ray, and biserial brachials in mature arms.

Description.—Crown and aboral cup small in size for *Platycrinites*; calyx plate sculpturing smooth, sutures not depressed. Basal circlet high, approximately 33 percent of cup height; base concave, truncate; proximal column in basal concavity; ridge around margin of basal concavity (Fig. 10.6). Radial circlet approximately 67 percent of cup height. Radial plates five, slightly wider than high. Radial facet approximately 50 percent of distal radial plate width. Details of radial facet unknown. Tegmen unknown.

As known, five robust arms per ray. First primibrachial axillary, full width of radial facet; first secundibrachial uniserial, quadrangular, not in contact medially with adjacent secundibrachial; second secundibrachial axillary on both half-rays. On one half-ray one further division on abmedial quarter-ray, second tertibrachial axillary, both tertibrachials quadrangular uniserial, quartibrachials cuneate uniserial before becoming biserial; other half-ray unbranched, brachials cuneate uniserial before becoming biserial. Pinnules and column unknown.

Material examined.—Holotype of *P.* s.l. *contritus* NYSM 6134. CMNH 5821c questionably assigned to this species.

Occurrence.—*Platycrinites* s.l. *contritus* from the Meadville Shale Member of the Cuyahoga Formation in northeastern Ohio at Richfield.

Discussion.—An illustration of this 1863 species was not produced until Hall and Whitfield (1875, pl. 11, fig. 4). As the only specimen from that era, this specimen is regarded as the holotype. See discussion in *Platycrinites* that distinguishes this species from other Meadville *Platycrinites.*

Measurements.—See Table 6.

PLATYCRINITES s.l. GRAPHICUS (Hall, 1863)
Figures 7.2, 7.3, 9.4–9.7

Platycrinus graphicus HALL, 1863, p. 55; SHUMARD, 1868, p. 388; HALL AND WHITFIELD, 1875, p. 166, pl. 11, fig. 2; MILLER, 1889, p. 271; LESLEY, 1889, p. 687, fig. 2; WACHSMUTH AND SPRINGER, 1897, p. 672, pl. 71, fig. 7; MILLER, 1897, p. 750; WELLER, 1898 p. 439.
Platycrinites graphicus (HALL, 1863b). BASSLER AND MOODEY, 1943, p. 621; WEBSTER, 2003.

←

FIGURE *10—Halysiocrinus sp., Platycrinites* s.l. *burkei* n. sp., and *Platycrinites* s.l. *contritus*. *1*, *2*, *Halysiocrinus* sp., CMNH 5585b: *1*, posterior side of compressed crown, prominent plates are anal series, enlargement of *Fig. 10.2*, ×3.0; 2, compressed crown on distal arms of *Platycrinites* s.l. *burkei,* see *Fig. 9.1; 2–7*, *Platycrinites* s.l. *burkei* n. sp.: *2*, lateral view of crown, holotype, note *Halysiocrinus* sp. in distal arms holotype, CMNH 5585a, ×2.0; *3,* calyx and proximal arms, note distinctive plate sculpturing, paratype, CMCIP 46144, ×3.5; *4*, lateral view of crown, paratype, CMCIP 46144, ×1.0; *5*, calyx and proximal arms, note distinctive plate sculpturing, paratype, CMNH 5083, ×3.5; *7*, lateral view of crown, paratype, CMNH 5083, ×1.0; *6, Platycrinites* s.l. *contritus*, lateral view of holotype, NYSM 6134 (previously illustrated in Hall and Whitfield, 1875, pl. 11, fig. 4), ×1.5.

TABLE 6—Measurements for *Platycrinites* s.l. (in mm, * incomplete or specimen compacted, ** holotype or neotype).

Specimen	Crown height	Calyx height	Calyx width	Basal plate height	Basal plate width	Radial plate height	Radial plate width	Primaxil height	Primaxil width
P. burkei n. sp.									
CMCIP 46144	70.8	19.2	—	3.3	8.6*	8.2	9.3	1.5	4.4
CMCIP 46077g	—	8.7	—	1.7		4.9	6.7	1.6	3.0
CMNH 5083	71.1	18.0	20.4	6.1	15.1	12.8	8.8	2.0	4.3
CMNH 5585a**	66.0	14.0	19.4	5.4	13.8	8.5	9.1	1.4	3.9
P. contritus									
NYSM 6134**	30.7	9.6	—	2.5	5.5	4.6	8.6	1.9	4.0
P. graphicus									
NYSM 6135**	62.0	13.0	—	6.5	9.1	6.8	9.4	1.8	4.0
CMCIP 46145	—	—	—	3.6	5.7	6.9	7.4	1.8	3.1
CMCIP 46146	—	—	—	3.3	6.9	6.6	8.6	2.2	3.2
CMCIP 46147a	38.4	7.1	10.5	2.8	6.8	4.3	5.2	1.4	2.1
CMCIP 46148	—	—	—	3.3	5.1	5.4	5.8	1.2	2.4
CMCIP 46149A	22.8	5.1	—	0.9	2.0	2.3	2.9	1.5	2.0
CMNH 5928	50.0	9.5	7.4	3.4	10.1	7.7	7.0	1.9	3.8
P. lodensis									
CMCIP 46143**	22.8	5.1	—	3.6	8.5	7.2	10.0	1.8	5.6

Platycrinus richfieldensis HALL AND WHITFIELD, 1875, p. 167, pl. 11, fig. 1; MILLER, 1889, p. 271; LESLEY, 1889, p. 689, fig. 1; MILLER, 1897, p. 750; WELLER, 1898, p. 439; BASSLER AND MOODEY, 1943, p. 621; WEBSTER, 2003.

Platycrinites s.l. *graphicus* (HALL, 1863). AUSICH AND KAMMER, 2009, p. 704.

Diagnosis.—Calyx plate sculpturing smooth, convex basal circlet, radial plate approximately 1.25 times wider than high, radial facet approximately 33 to 50 percent radial plate width, details of radial facet unknown, four typically gracile arms per ray (rarely less gracile or five arms), and biserial brachials in mature arms.

Description.—Crown and aboral cup small to medium in size for *Platycrinites*; smooth calyx plate sculpturing, sutures not depressed. Basal circlet high, approximately 25 percent cup height; low to flat bowl shape; short neck above column attachment; smooth. Basal plates three, unequal in size (two large, one small). Radial circlet approximately 75 percent of cup height. Radial plates five, approximately 1.25 times wider than high (although equidimensional in juveniles). Radial facet width variable, ranging from approximately 33 to 50 percent of distal radial plate width (holotype and most specimens 50 percent), details of radial facet unknown. Tegmen unknown.

Arms four (rarely five) per ray, gracile (rarely more robust) (Fig. 9.4, 9.7). First primibrachial axillary, full width of radial facet; first secundibrachial uniserial, quadrangular, not in contact medially with adjacent secundibrachial (Fig. 9.7); second secundibrachial axillary; proximal tertibrachials cuneate uniserial then biserial (Fig. 7.2, 7.3). Pinnules long, slender.

Column helically twisted (Fig. 9.6); proxistele heteromorphic, one nudinodal separated by one priminternodal; columnals elliptical, low; latera smooth, strongly convex. Mesistele homeomorphic; columnals elliptical, slightly higher than wide, constricted medially; dististele columnals similar in size and shape to those of mesistele, one or two rhizoid from narrow side of columnal (Fig. 9.5), distal few columnals only slightly elliptical in cross section.

Material examined.—Holotype NYSM 6135 from Richfield. Additional Richfield specimens: CMCIP 46113, 46145–46149 (with the latter a juvenile), 46153, and 46154. Lodi specimens: CMNH 5679, 5685a, 5885a–5885c, CMNH 5905a, and CMNH 5913. CMNH 5928 and CMCIP 4651 questionably assigned to this species.

Occurrence.—*Platycrinites* s.l. *graphicus* from the Meadville Shale Member of the Cuyahoga Formation in northeastern Ohio from Lodi and Richfield.

Discussion.—Again, the only specimen illustrated by James Hall was Hall and Whitfield (1875, pl. 11, fig. 2). This specimen NYSM 6135 is regarded as the holotype.

The compressed holotype of *P.* s.l. *graphicus* (Fig. 9.4) makes the basal circlet appear much higher (relative to the radial circlet) than it actually is. The right margin of the holotype is regarded, herein, to be more representative of the relative heights of the basal circlet versus the radial circlet. The holotype of *P. richfieldensis* (Hall and Whitfield, 1875) (=junior synonym of *P. graphicus*) was not located, but we also regard this specimen to have been compressed to yield a false apparent height of the basal circlet.

The discussion of *Platycrinites* s.l. includes the differentiation of this species from other *Platycrinites* s.l. in the Meadville Shale.

Measurements.—See Table 6.

PLATYCRINITES s.l. LODENSIS (Hall and Whitfield, 1875)
Figures 7.7, 11.1–11.4

Platycrinus lodensis HALL AND WHITFIELD, 1875, p. 168, pl. 2, fig. 3; MILLER, 1889, p. 271; WACHSMUTH AND SPRINGER, 1897, p. 666, pl. 71, fig. 6; WELLER, 1898, p. 441.

Platycrinus lodiensis (HALL AND WHITFIELD, 1875) [sic.]. LESLEY, 1889, p. 688, fig. 3; AUSICH, 1996, p. 249, fig. 17-7.2, 17-7.3.

Platycrinites lodensis (HALL AND WHITFIELD, 1875). BASSLER AND MOODEY, 1943, p. 623; WEBSTER, 2003.

Platycrinites s.l. *lodensis* (HALL AND WHITFIELD, 1875). AUSICH AND KAMMER, 2009, p. 704.

Diagnosis.—Calyx plate sculpturing smooth, typically convex basal circlet, radial plate as high as wide, radial facet approximately 50 percent of radial plate width, details of radial facets unknown, four robust arms per ray, and biserial brachials in mature arms.

Description.—Crown and aboral cup medium in size for *Platycrinites*; plates smooth sculpturing, sutures not depressed (Fig. 10.4). Basal circlet high, approximately 25 percent of cup height (Fig. 11.1, 11.2); calyx base convex; may have low neck above column attachment. Details of basal plates unclear. Radial circlet approximately 75 percent of cup height (Fig. 10.3). Radial plates five, approximately as high as wide. Radial facet approximately 50 percent of distal radial plate

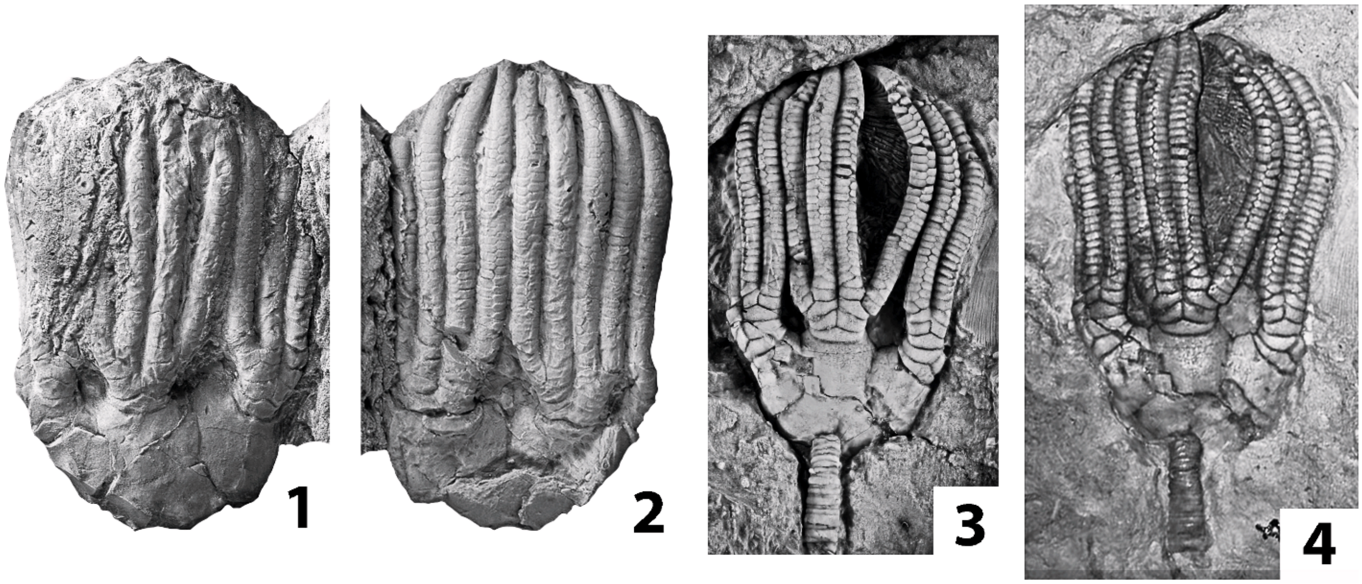

FIGURE *11*—*Platycrinites* s.l. *lodensis*. *1*, *2*, lateral view of both sides of compressed calyx, neotype, CMCIP 46143; *3*, *4*, lateral view of crown (compare to *Fig. 7.7*), neotype, CMCIP 5748, ×1.25; *3*, coated; *4*, uncoated.

width, declivate, steeply inclined abaxially. Details of radial facet not known. Tegmen not known.

Arms four robust (Figs. 7.7, 10.3). First primibrachial axillary, low, full width of radial facet; first secundibrachial uniserial, quadrangular, in sutural contact medially with adjacent first secundibrachial (Figs. 7.7, 10.4, 10.7); second secundibrachial axillary; first or second tertibrachial cuneate, above which all brachials biserial. Pinnules not known.

Column not known.

Discussion.—For differentiation of this species from other sympatric congeners, see discussion of *Platycrinites* s.l. above.

Material examined.—Holotype not located. CMCIP 46143, from Richfield, designated, herein, neotype (Fig. 11.1, 11.2). Additional specimens from Lodi: CMNM 5582; 5583a, 5583b; 5685b; 5704; 5747b; 5885d, 5885e; 5928; 5934; 5935; 5953; 5954b; 5956a; 5975; 12142; 12156; 12162; and 12284. CMNM 5880h questionably assigned to this taxon.

Occurrence.—*Platycrinites* s.l. *lodesnsis* from the Meadville Shale Member of the Cuyahoga Formation in northeastern Ohio from Lodi and Richfield.

Measurements.—See Table 6.

PLATYCRINITES s.l. BURKEI new species
Figure 10.2–10.5, 10.7

Diagnosis.—Calyx plate sculpturing with fine, irregular ridges radiating from radial facets; convex basal circlet; radial plates higher than wide; radial facet approximately 50 percent radial plate width; details of radial facet not known; six gracile arms per ray, and biserial brachials in mature arms.

Description.—Crown and aboral cup medium in size for *Platycrinites*; calyx plate sculpturing with fine, irregular ridges radiating from radial facets or from base of basal circlet (Fig. 10.3, 10.5); sutures not depressed. Basal circlet high, approximately 25 percent cup height (Fig. 10.7), base low bowl with short neck above column attachment. Basal plates three, unequal in size (two large, one small). Radial circlet approximately 75 percent cup height. Radial plates five, approximately 1.25 times higher than wide. Radial facet approximately 50 percent distal radial plate width. Details of radial facet unknown. Tegmen unknown.

Six gracile free arms per ray (Fig. 10.2, 10.4). First primibrachial axillary, low, full width of radial facet; first secundibrachial uniserial, quadrangular, not in contact medially with adjacent first secundibrachial (Fig. 10.3, 10.5); second secundibrachial axillary, endotomous arm branching on abmedial branch, above secundaxil atomous cuneate uniserial before becoming biserial. Admedial branch with two tertibrachials before isotomous branch; tertibrachials quadrangular uniserial; quartibrachials cuneate uniserial brachials before becoming biserial. Pinnules long, slender (Fig. 10.7).

Proximal column helically twisted; heteromorphic, one nudinodal separated by one priminternodal. Columnals elliptical; latera smooth, very convex (Fig. 10.7); mesistele and dististele unknown.

Discussion.—Discussion of *Platycrinites* s.l. above includes differentiation among Meadville Shale species.

Etymology.—The species name recognizes John J. Burke for his contributions to the study of Carboniferous crinoids from Ohio.

Material examined.—Holotype CMCH 5585a, from Lodi. Paratypes: CMNH 5803 (Lodi) and CMCIP 46144 (Richfield). Additional specimens from Richfield: CMCIP 46061 and 46077g. Specimens from Lodi: CMNM 3786; CMNM 5584; CMNM 5682; CMNM 5688; CMNM 5797; CMNM 5820k; CMNM 5828a, 5828b; CMNM 5910; CMNM 5954b; CMNM 12266a, 12266b; and CMNM 12283b. CMNH 4410 and CMCIP 46152 questionably assigned to this species.

Occurrence.—*Platycrinites* s.l. *burkei* from the Meadville Shale Member of the Cuyahoga Formation in northeastern Ohio from Lodi and Richfield.

Measurements.—See Table 6.

Subclass DISPARIDA Moore and Laudon, 1943
Order CALCEOCRINIDA Ausich, 1998
Family CALCEOCRINIDAE Meek and Worthen, 1869
Genus HALYSIOCRINUS Hall, 1852

Type species.—Cheirocrinus dactylus Hall, 1860.

HALYSIOCRINUS sp.
Figure 10.1, 10.2

Discussion.—A single specimen of *Halysiocrinus* is known from the Meadville Shale. This specimen is adhered to the

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distal arms of the holotype of *P. burkei* n. sp. (Fig. 10.2). This *Halysiocrinus* specimen is preserved in a very unusual manner; it is compressed adanally-abanally with the anal side exposed (Fig. 10.1). The basal circlet and the anal sac are well exposed, but the details of the lateral arms, E-ray arm, and radial circlet are not exposed.

Although not completely known, this crinoid is confidently considered a *Halysiocrinus* based on the following diagnostic characters from Harvey and Ausich (1997): perfect bilateral symmetry, recumbent posture, aborally-adorally compressed aboral cup, three basal plates, B and C inferradials absent, main axil series lacking nonaxillary brachials, three arms, lateral arms heterotomous, and a gracile beta ramule. However, a sufficient number of E-ray arm and lateral arm characteristics are unknown, so that a species designation cannot be made.

Material examined.—Single specimen (CMNH 5585b) preserved in the distal arms of the holotype of *P.* s.l. *burkei*.

Occurrence.—*Halysiocrinus* sp. from the Meadville Shale Member of the Cuyahoga Formation at Lodi in northeastern Ohio.

Measurements.—Crown height, 18.9*; calyx height, 7.6; calyx width, 5.8.

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ACCESSIBILITY OF SUPPLEMENTAL DATA

Supplemental data deposited in Dryad data package
http://datadryad.org/handle/10255/dryad.38066
doi:10.5061/dryad.kn8b72m5

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