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Disparid and hybocrinid crinoids (Echinodermata) from the Upper Ordovician (lower Katian) Brechin Lagerstätte of Ontario

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Abstract.—The Brechin Lagerstätte (Katian, Ordovician) from the Lake Simcoe region of Ontario, Canada contains a diverse array of echinoderms. Here, we describe seven disparid and two hybocrinid crinoids (subclass Pentacrinoidea, infraclass Inadunata), including a new disparid species belonging to the Anomalocrinidae (order Homocrinida). In total, the disparids include *Anomalocrinus astrictus* n. sp.; *Cremacrinus guttenbergensis* Kolata, 1975; *C. inaequalis* Billings, 1859; *Daedalocrinus bellevillensis* Billings, 1883; *Eustenocrinus springeri* Ulrich, 1925; *Iocrinus trentonensis* Walcott, 1883; and *Isotomocrinus tenuis* Billings, 1857b. The hybocrinids include *Hybocrinus tumidus* Billings, 1857a and *Hybocystites problematicus* Wetherby, 1880. Previously known from only the holotype, three additional specimens of *E. springeri* expand our understanding of this unusual crinoid. Nomenclatural acts include: (1) the recommended designation of *D. kirki* Ulrich, 1925 as a junior synonym of *D. bellevillensis* is followed; (2) *Hybocrinus pristinus* Billings, 1858 is designated as a junior synonym of *H. tumidus*, and previous decisions are followed to retain *Hybocystites eldonensis* (Parks, 1908) as a junior synonym of *H. problematicus*; (3) although probably assignable to *Anomalocrinus* Meek and Worthen, 1865, the aberrant crinoid *Glaucocrinus falconeri* Parks and Alcock, 1912, and its genus *Glaucocrinus* Parks and Alcock, 1912, are designated as nomena dubia; (4) *Iocrinus similis* (Billings, 1857) is also designated as a nomen dubium; and (5) *Iocrinus subcrassus torontoensis* Fritz, 1925 is designated a junior synonym of *I. subcrassus* Meek and Worthen, 1865.

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Introduction

Upper Ordovician (lower Katian) rocks from the upper Bobcaygeon–lower Verulam Formation interval in the Lake Simcoe region of Ontario, Canada are well known for their exceptionally preserved echinoderm fauna and for well-exposed hardgrounds that supported a diverse shallow-marine fauna. Numerous taxa in this fauna are known completely, from the arms/brachials to the attachment structure, which is most unusual and why we refer to this fauna as the Brechin Lagerstätte (Cole et al., 2018).

Study of upper Bobcaygeon Formation–lower Verulam Formation echinoderms began with the work of Billings (1856, 1857a, 1858, 1859). Further, several studies have addressed the paleoecology of this remarkable echinoderm occurrence (e.g., Brett and Liddell, 1978; Brett and Brookfield, 1984; Brett and Taylor, 1999; Brett et al., 2008). However, the last general systematic evaluation of the entire crinoid fauna was by Springer (1911). Since then, the systematics of a few taxa have been studied (e.g., Guensburg, 1992), but a comprehensive taxonomic evaluation is much needed. This study is part of a larger reevaluation of crinoids from the Brechin Lagerstätte. This contribution considers only the disparid and hybocrinid crinoids (subclass Pentacrinoidea, infraclass Inadunata) and is preceded by that of Cole et al. (2018), which evaluated the dicyclic camerate crinoids (subclass Camerata) of the Brechin Lagerstätte. Future studies in this series will include a re-evaluation of monocyclic camerate crinoids and all other species belonging to the Pentacrinoidea (e.g., eucladids and flexibles, see Wright et al., 2017).

Katian crinoid faunas are of particular importance to our understanding of crinoid evolutionary history because they represent upper tiering levels of communities at the culmination of the Great Ordovician Biodiversification Event (GOBE; Webby et al., 2004; Ausich and Deline, 2012; Wright and Toom, 2017). These faunas are from the final stages of the early Paleozoic crinoid evolutionary fauna and are among the last faunas that thrived in shallow epicontinental seas prior to the Late Ordovician extinctions that resulted from global climate change and habitat destruction (e.g., Sheehan, 2001; Brenchley et al., 2003; Peters and Ausich, 2008).

In this paper, we describe all known disparid and hybocrinid crinoids from the Brechin Lagerstätte, including a new species of disparid belonging to the Anomalocrinidae (order Homocrinida). Our descriptions and taxonomic reassessments include the disparids *Anomalocrinus astrictus* n. sp.; *Cremacrinus guttenbergensis* Kolata, 1975; *Cremacrinus inaequalis* Billings, 1859; *Daedalocrinus bellevillensis*

Billings, 1883; *Eustenocrinus springeri* Ulrich, 1925; *Iocrinus trentonensis* Walcott, 1883; and *Isotomocrinus tenuis* Billings, 1857b; and the hybocrinids *Hybocrinus tumidus* Billings, 1857a and *Hybocystites problematicus* Wetherby, 1880. Warn and Strimple (1977) recommended that *D. kirki* Ulrich, 1925 is a junior synonym of *D. bellevillensis*. We follow this recommendation. *Hybocrinus pristinus* Billings, 1858 is designated as a junior synonym of *H. tumidus*. The recommendation by Springer (1911) and the action by Parsley (1981), that *Hybocystites eldonensis* (Parks, 1908) is a junior synonym of *Hybocystites problematicus*, are followed. Although probably assignable to *Anomalocrinus* Meek and Worthen, 1865 (see also Guensburg, 1992), the aberrant crinoid *Glaucocrinus falconeri* Parks and Alcock, 1912 is designated a nomen dubium; *Iocrinus similis* (Billings, 1857a) is also designated a nomen dubium.

Geologic setting

Stratigraphic nomenclature for the Ordovician of southern Ontario has changed substantially with time, and today it remains unsettled. Further, outcrop versus subsurface nomenclature is typically different. Herein, we primarily follow the outcrop lithostratigraphic nomenclature of Armstrong (2000). The new crinoid specimens considered herein are from the Lake Simcoe region and the Bobcaygeon and Verulam formations, which are part of the middle portion of the Lake Simcoe Group (the Lake Simcoe Group is equivalent to the Trenton and Ottawa groups, see Armstrong, 2000). The middle and upper Bobcaygeon Formation and the lower Verulam Formation are Late Ordovician (Katian) in age (Brookfield and Brett, 1988; Holland and Patzkowsky, 1996; Sproat et al., 2015).

Older literature reports crinoids from the Kirkfield, Hull, and Cobourg units. The Hull Formation of previous workers is now considered equivalent to the upper Bobcaygeon Formation. Similarly, the Kirkfield Formation of previous workers is now considered equivalent to the middle–upper Bobcaygeon Formation. The Cobourg beds of previous workers is now considered equivalent to the lower member of the Lindsay Formation, which is superjacent to the Verulam Formation. For further discussion of the stratigraphic nomenclature, sedimentology, taphonomy, and history of the study of the Brechin Lagerstätte, see Cole et al. (2018).

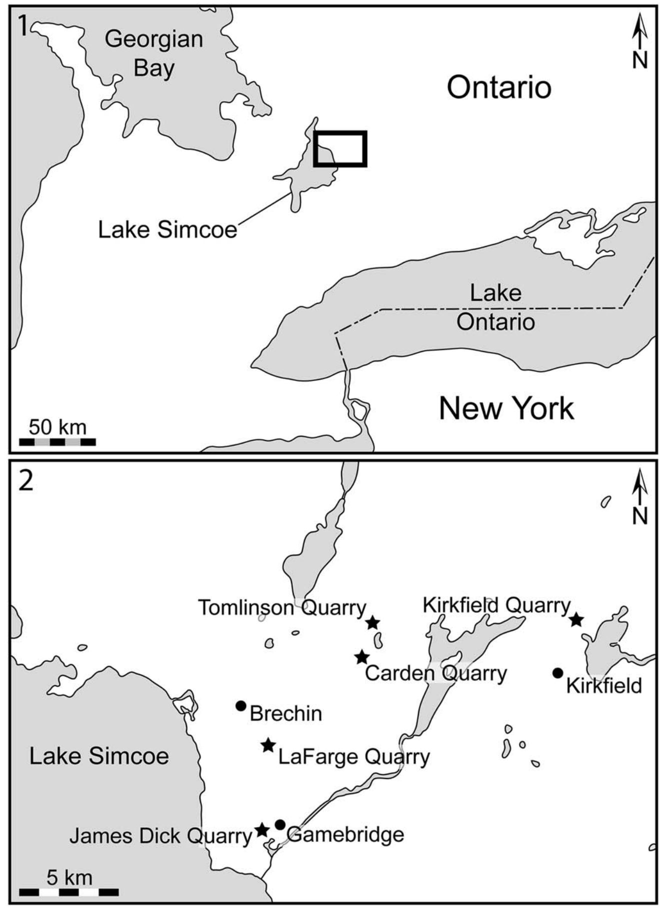

Figure 1. Location map with position of various quarries in the Lake Simcoe region of southern Ontario from which crinoids of the Brechin Lagerstätte are known: (**1**) southern Ontario with study area in box; (**2**) relative position of collection sites (stars) within the study area. Modified from Cole et al. (2018).

Materials and methods

Localities.—New material reported herein was collected from active quarries. With specimens recovered from blast piles, the upper Bobcaygeon-Verulam Formation boundary interval is commonly the most precise stratigraphic placement possible, because this is the fossiliferous part of the section. More precise stratigraphic data are given where possible. All material is from the vicinity of Brechin, Ontario, Canada. Quarries from which new crinoids from the J.M. Koniecki collection were recovered include the Carden Quarry (44°34'33.5"N, 79°06'09.5"W), located 6 km east of the town of Brechin; the LaFarge Quarry (44°31'55.9"N, 79°09'47.8"W), located 2 km southeast of Brechin; and the Tomlinson Quarry (44°35'45.9"N, 79°05'70.4"W), located 14 km northeast of Brechin. Additional material is from the James Dick Quarry (44°29'93.7"N, 79°09'61.6"W). Material from the Carden and LaFarge quarries was recovered from an unconstrained interval including ~15 m of upper Bobcaygeon and 5 m of lower Verulam (hereafter referred to as the 'Bobcaygeon-Verulam contact zone'); material from the Tomlinson Quarry is from the upper Bobcaygeon; and material from the James Dick Quarry is from the lower Verulam. Older collections in the Lake Simcoe region are predominately from the upper Bobcaygeon of the classic Kirkfield Quarry (44°35'06.32"N, 78°58'08.16"W), which is now flooded and inaccessible (Fig. 1).

Repositories and institutional abbreviations.—New specimens for this study are deposited in the University of Michigan Museum of Paleontology (UMMP). Depository of other specimens considered here include: BMNH, Burpee Museum of Natural History, Rockford, Illinois, USA; CMC IP, Cincinnati Museum Center Invertebrate Paleontology Collections, Cincinnati, Ohio, USA; GSC, Geological Survey of Canada, Ottawa, Canada; MCZ, Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; ROM, Royal Ontario Museum, Toronto, Canada; USNM S, Springer Room, National Museum of Natural History, Washington, DC, USA.

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Systematic paleontology

The classification used herein follows the phylogeny-based revision of crinoid higher taxa by Wright et al. (2017). Recent phylogenetic analyses find disparids to be sister to the Cladida, with hybocrinids nested within the Cladida and sister to the porocrinids (Ausich et al., 2015; Wright, 2017). At higher taxonomic scales, both disparids and hybocrinids belong to the infraclass Inadunata, which is placed within the newly resurrected subclass Pentacrinoidea (Wright et al., 2017). Morphological terminology follows Ubaghs (1978) and Ausich et al. (1999), with modifications from Ausich (1996, 1998) and Ausich et al. (2015). Plate diagrams for the genera treated in this study are given in Supplemental Data. Abbreviations used in designating measurements include: ACH, aboral cup height; ACW, aboral cup width; AH, arm height; ASH, anal sac height; CaH, calyx height; CoH, column height; and CrH, crown height. All measurements are given in mm; an asterisk (*) indicates that a measurement is of a partial or compacted specimen.

Class Crinoidea Miller, 1821
Subclass Pentacrinoidea Jaekel, 1894
Infraclass Inadunata Wachsmuth and Springer, 1885
Parvclass Disparida Moore and Laudon, 1943
Order Eustenocrinida Ausich, 1998
Family Eustenocrinidae Ulrich, 1925

Genus *Eustenocrinus* Ulrich, 1925

Type species.—*Eustenocrinus springeri* Ulrich, 1925, by monotypy.

Occurrence.—Ordovician (Katian), Ontario, Canada.

Remarks.—In many ways, *Eustenocrinus* is an iconic Ordovician crinoid. It has an unusual morphology that defines an order-level taxonomic rank with compound radial plates in all five rays, only four functional arms, and the anal sac seated directly on the C radial plate. However, *Eustenocrinus* is a monospecific genus, and its only species, *E. springeri*, is relatively poorly documented. Prior to the present study, we were aware of only a single specimen (the holotype) of this taxon. Ulrich (1925) illustrated his new taxon with only line drawings: one a plate diagram and the other of a partial crown in lateral view. With the exception of Moore and Lane (1978a, fig. 347.1c, d), all subsequent authors have illustrated *E. springeri* with either a reproduction or modification of Ulrich's original drawings. The exceptions are photographs of two sides of the holotype (USNM S 2148) by Moore and Lane (1978a).

The holotype is a partial crown that has been prepared to be loose from the matrix. The two parts of this specimen include the separated partial aboral cup that includes inferradial plates to the proximal secundibrachials (Fig. 2.1, 2.2). The proximal column is still embedded in the matrix and includes the attached basal circlet (Fig. 2.3). Thus, the three new specimens documented herein from the Brechin fauna add significantly to our understanding of this important Ordovician crinoid. Two specimens (UMMP 74652 and 74653) are partial crowns with some column attached, and the third specimen (UMMP 74654) is a set of complete or nearly complete arms.

Eustenocrinus springeri Ulrich, 1925
Figures 2, 3

1925 *Eustenocrinus springeri* Ulrich in Foerste, p. 99, fig. 14.
1938 *Eustenocrinus springeri*; Bassler, p. 99.
1943 *Eustenocrinus springeri*; Bassler and Moodey, p. 474.
1953 *Eustenocrinus springeri*; Ubaghs, p. 744, fig. 18a, b.
1964 *Eustenocrinus springeri*; Yakovlev, p. 66, fig. 92a.
1973 *Eustenocrinus springeri*; Webster, p. 129.
1978 *Eustenocrinus springeri*; Ubaghs, p. T122, fig. 93.1, 93.2.
1978a *Eustenocrinus springeri*; Moore and Lane, p. T553, fig. 347.1.
1986 *Eustenocrinus springeri*; Webster, p. 147.
2013 *Eustenocrinus springeri*; Webster and Webster, p. 1477.

Holotype.—USNM S 2148.

Diagnosis.—Disparid with compound radials in all five rays; four free arms, one each in A, B, D, and E rays; anal series articulated directly above the C superradial plate.

Occurrence.—*Eustenocrinus springeri* was originally described from the 'lower Trenton' at Kirkfield, Ontario, Canada, which is stratigraphically equivalent to the upper Bobcaygeon Formation. New material is from the Bobcaygeon-Verulam contact zone at the Carden Quarry (UMMP 74654) and from an uncertain location but probably the Carden Quarry (UMMP 74652, UMMP 74653) (Ordovician, Katian).

Description.—Crown large, cylindrical when in closed, trauma posture (Fig. 2.1). Aboral cup small, subcylindrical, but constricted at basal circlet-inferradial circlet juncture (Fig. 2.5), approximately of same diameter at proximal column (Fig. 2.6); width to height ratio ~1.0–2.0; plates gently convex, sculpture smooth.

Basal circlet ~30% of aboral cup height; basal plates five, pentagonal, slightly wider than high. Radial circlet ~70% of aboral cup height; radial plates five, all compound. Inferradial plates as high as wide; superradials slightly wider than high. Radial facet plenary with first primibrachial sutured into calyx (Fig. 3.3).

Anal X only anal plate in cup, indistinguishable from first primibrachial, sutured immediately above C radial plate, approximately as wide as high (Fig. 3.4). More distal anal plates above anal X similar to brachials.

Arms four, extremely long (Fig. 2.8), branching once isotomously on seventh or eleventh primibrachial (Fig. 2.4, 2.7).

Figure 2. *Eustenocrinus springeri* Ulrich, 1925: (**1–3**) holotype, USNM S 2148; (**1**) AB interray view of partial crown (radial circlet at the bottom to proximal secundibrachials); (**2**) C ray (note anal sac directly above C superradial plate) view of partial crown (radial circlet at the bottom to proximal secundibrachials); (**3**) lateral view of partial column with attached basal circlet; (**4**) UMMP 74653, lateral view of partial crown and column (note indentation at basal circlet-inferradial circlet junction); (**5–6**) UMMP 74652; (**5**) enlargement of C ray (note anal sac directly above C superradial plate) lateral view of crown and proximal column; (**6**) entire preserved specimen; (**7–8**) nearly complete set of arms assigned to *E. springeri*, UMMP 74654; (**7**) enlargement of proximal rays; (**8**) arms (note long, gracile ramules). Scale bars = 2.5 mm (**1–3, 5, 7**); 5.0 mm (**4, 6, 8**).

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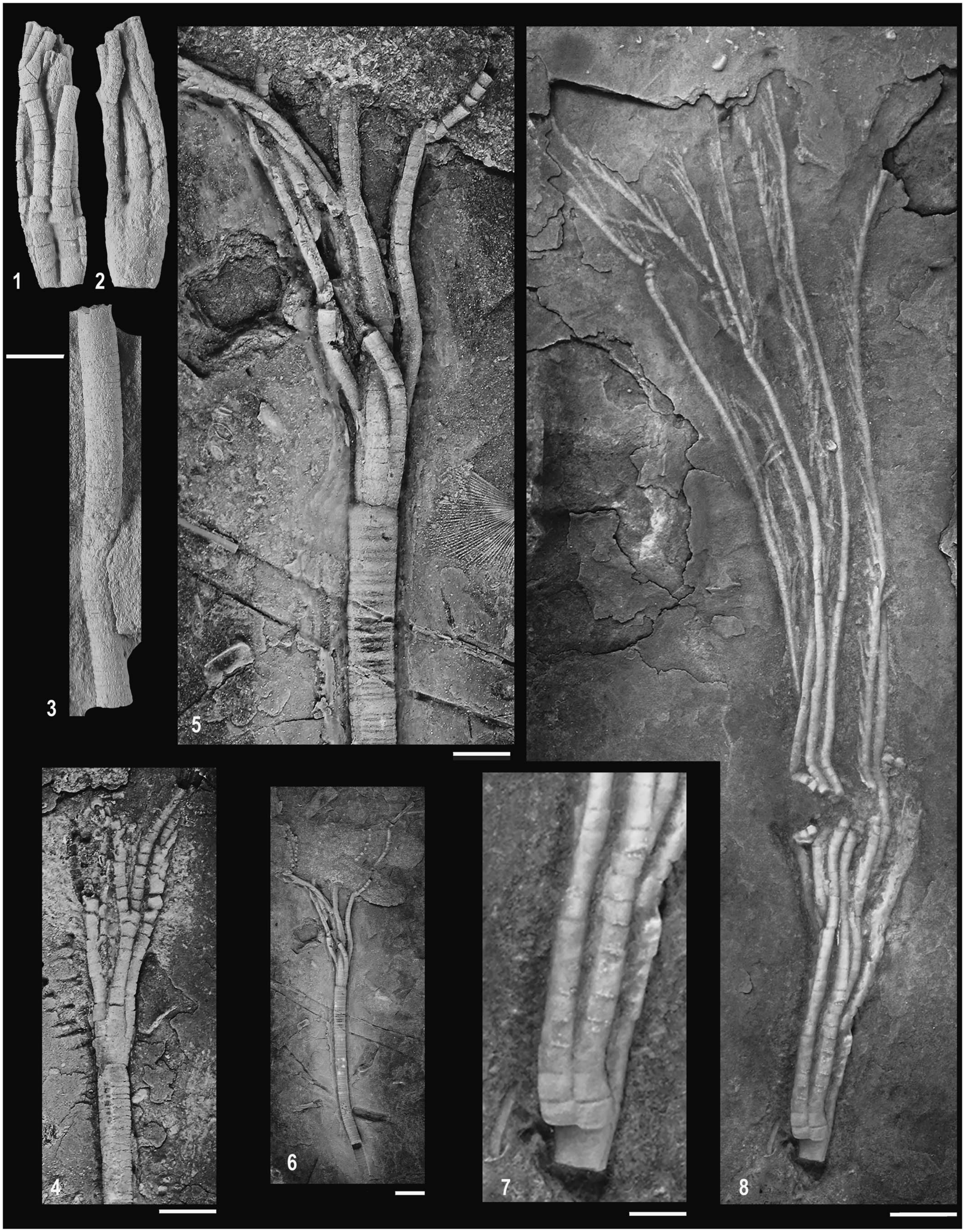

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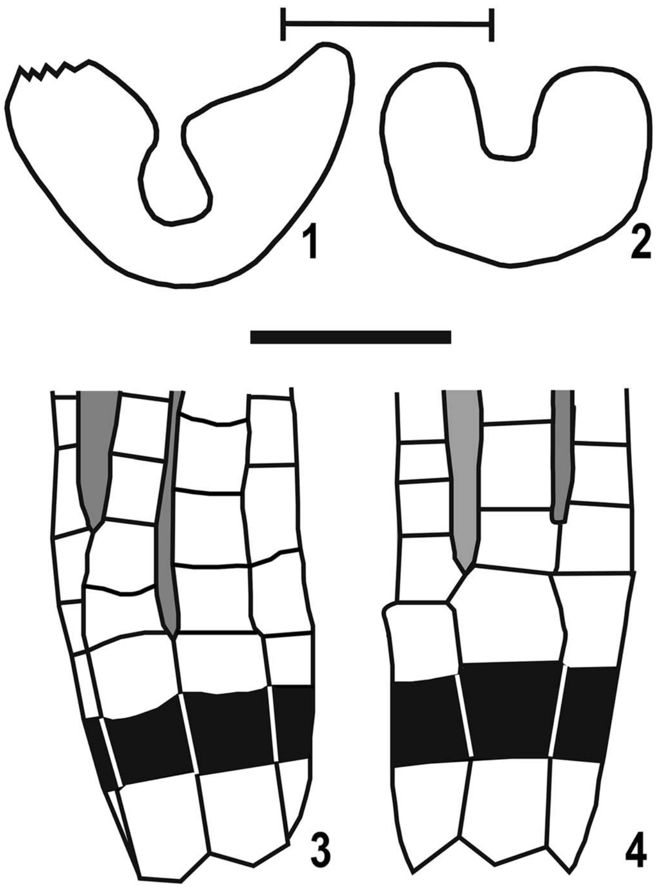

Figure 3. *Eustenocrinus springeri* Ulrich, 1925, USNM S 2148, camera lucida drawings: (**1, 2**) Cross-sectional shapes of 'appendages'; (**1**) cross section of a plate from the dominant column of anal sac plates; (**2**) cross section of brachial on E-ray arm; (**3, 4**) plate diagrams; (**3**) AB interray lateral view, compare to Figure 1.1; (**4**) CD interray lateral view, compare to Figure 1.2. Black filling, superradial plates; horizontal ruling, infraradial plates; gray shading, matrix. Scale bar = 1.0 mm.

First primibrachial completely or partially fixed; nonaxillary primibrachials and more proximal secundibrachials approximately as wide as high, gently convex; more distal brachials can be higher than wide. Ramules typically branching from every third secundibrachial; ramules branching endotomously (as presently known). Ramules very long and narrow; ramulars higher than wide.

Column > 40 mm long, circular, heteromorphic (Fig. 2.5), cryptically pentameric. Series of circular, dark calcite structures (infilling of pores) along cryptic pentamere sutures more or less at position of secundinternodals; pore openings of canals penetrating into column. Heights of nodals and internodals irregular; N212 most common columnal arrangement. Lumen pentagonal; details of columnal facets unknown.

Materials.—UMMP 74652–74654; USNM S 2148.

Measurements.—USMN S 2148: ACH, 2.7; ACW, 2.7; AH, 10.6*; CoH, 18.0*. UMMP 74652: ACH, 3.0; ACW, 2.33; AH, 33.0*; CoH, 36.0*. UMMP 74653: ACH, 3.0*; ACW, 1.5; AH, 10.6*; CoH, 18.0*.

Remarks.—With this new material from the Brechin Lagerstätte, this important Ordovician taxon can be more completely characterized, and at least some aspects of its intraspecific variability can be understood. This is especially true for the arms that are extremely high for a crinoid with such a small aboral cup. Also, the unusual morphology of the column can be described. As noted in the description, the column is cryptically pentameric, and aligned with the pentamere sutures is a series of circular structures filled with a dark matrix. One broken portion of the column reveals that this structure is an unbranched canal penetrating from the outside into the column. To fully detail the morphology of these canals, columns would need to be sectioned. However, because of the scarcity of specimens of *Eustenocrinus springeri*, this was not done.

In the traditional (Ulrich, 1925) interpretation, *Eustenocrinus* has five compound radial plates, four free arms, and the anal series sutured directly above the C superradial. This represents a unique crinoid morphology, and alternative hypotheses discussed but rejected, herein, include: (1) *Eustenocrinus* has five arms with a small or absent anal sac; and (2) *Eustenocrinus* has simple radial plates. The appendage in the C ray is comprised of wider plates than brachials in the arms of other rays, and the cross-sectional shape of these ossicles differs from those of brachials. The groove on the C ray appendage is broader 'orally' and narrower and deeper 'aborally' than on the brachials of arms (Fig. 3.1, 3.2). Also note that the proximal C-ray plating is interlocked with adjacent rays (Figs. 2.5, 3.4) compared to the plating between rays with arms (Figs. 2.1, 3.3). Thus, it is reasonable to assume that this is a column of plates that supports an anal sac, as originally suggested by Ulrich (1925). This feature is also unusual because the proximal anal sac is flush with and enclosed laterally with adjacent arms before being encased distally within the arms (Fig. 2.2).

Eustenocrinus has been traditionally interpreted as having compound radial plates in all five rays, which is now recognized as a diagnostic character for the Eustenocrinidae. In *Eustenocrinus*, the delineation between the radial circlet and the brachials is not clear. However, in Figure 2.1, the sutures between the inferradials and superradials are well sutured, whereas, the superradial-first primibrachial sutures (as well as many brachial-brachial sutures) are somewhat askew. The material now available is more consistent with this taxon having five compound radial plates rather than five simple radial plates.

Order Homocrinida Ausich, 1998
Family Homocrinidae Kirk, 1914

Genus *Daedalocrinus* Ulrich, 1925

Type species.—*Daedalocrinus kirki* Ulrich, 1925, by monotypy. However, *D. kirki* is now regarded as a subjective junior synonym of *Heterocrinus bellevillensis* Billings, 1883 (see Warn and Strimple, 1977).

Occurrence.—Ordovician (Katian), Ontario, Canada.

Remarks.—In 1925, Ulrich named *Daedalocrinus* with his new species *D. kirki* as the type species. He also reassigned *Heterocrinus bellevillensis* as a species in *Daedalocrinus*. Ulrich (1925) distinguished these two species on the basis of size and robustness of the arms. *Daedalocrinus bellevillensis* had a large crown and robust arms and ramules, whereas *D. kirki*

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had a small crown with less robust arms and ramules. In the literature, both are listed from the Hull Limestone of Ontario.

Warn and Strimple (1977) completed the only reassessment of *Daedalocrinus* species since Ulrich (1925), and they regarded *D. kirki* to be a subjective junior synonym of *D. bellevillensis*. It is reasonable to view the differences between these nominal species that were highlighted by Ulrich (1925) as ontogenetic or as intraspecific differences; thus, herein, we follow the conclusions of Warn and Strimple (1977) and regard *Daedalocrinus* as a monospecific genus.

Daedalocrinus bellevillensis (Billings, 1883)
Figures 4.1–4.3, 5.1

1883 *Heterocrinus bellevillensis* Billings, p. 49, unnum. pl. and figs.
1889 *Heterocrinus bellevillensis*; Miller, p. 252.
1891 *Heterocrinus bellevillensis*; Wachsmuth and Springer, p. 392, pl. 10, fig. 8.
1899 *Heterocrinus bellevillensis*; Bather, p. 35, fig. 5.
1900 *Heterocrinus bellevillensis*; Bather, p. 146, fig. 58.2.
1886 *Stenocrinus bellevillensis*; Wachsmuth and Springer, p. 132 (p. 208).
1911 *Ohiocrinus bellevillensis*; Springer, p. 26.
1915 *Ohiocrinus bellevillensis*; Bassler, p. 870.
1915 *Stenocrinus bellevillensis*; Bassler, p. 870.
1925 *Daedalocrinus bellevillensis*; Ulrich, p. 83.
1925 *Daedalocrinus kirki* Ulrich, p. 97, fig. 13.
1938 *Daedalocrinus kirki*; Bassler, p. 83.
1943 *Daedalocrinus bellevillensis*; Bassler and Moodey, p. 404.
1943 *Daedalocrinus kirki*; Bassler and Moodey, p. 404.
1944 *Daedalocrinus kirki*; Moore and Laudon, p. 145, pl. 52, fig. 7.
1973 *Daedalocrinus kirki*; Webster, p. 98.
1977 *Daedalocrinus bellevillensis*; Warn and Strimple, p. 100, pl. 18, fig. 25.
1986 *Daedalocrinus bellevillensis*; Webster, p. 119.
2013 *Daedalocrinus bellevillensis*; Webster and Webster, p. 1245.

Holotype.—GSC 1439a, b.

Diagnosis.—Homocrinid with narrow cone-shaped crown, medium cone-shaped aboral cup, basal concavity absent, basal circlet low, all basal plates symmetrical, radial plates low, superradial plates not much lower than simple radial plates, arms ramulate, arm branching endotomous, proximal columnals low (from Ausich and Copper, 2010).

Occurrence.—The holotypes of both *Daedalocrinus bellevillensis* and *D. kirki* are from the 'lower Trenton' at Kirkfield, Ontario, Canada, which is stratigraphically in the upper Bobcaygeon Formation. New material from the Brechin Lagerstätte is from the Bobcaygeon-Verulam contact zone at the Carden Quarry (UMMP 74655–UMMP 74657) and the LaFarge

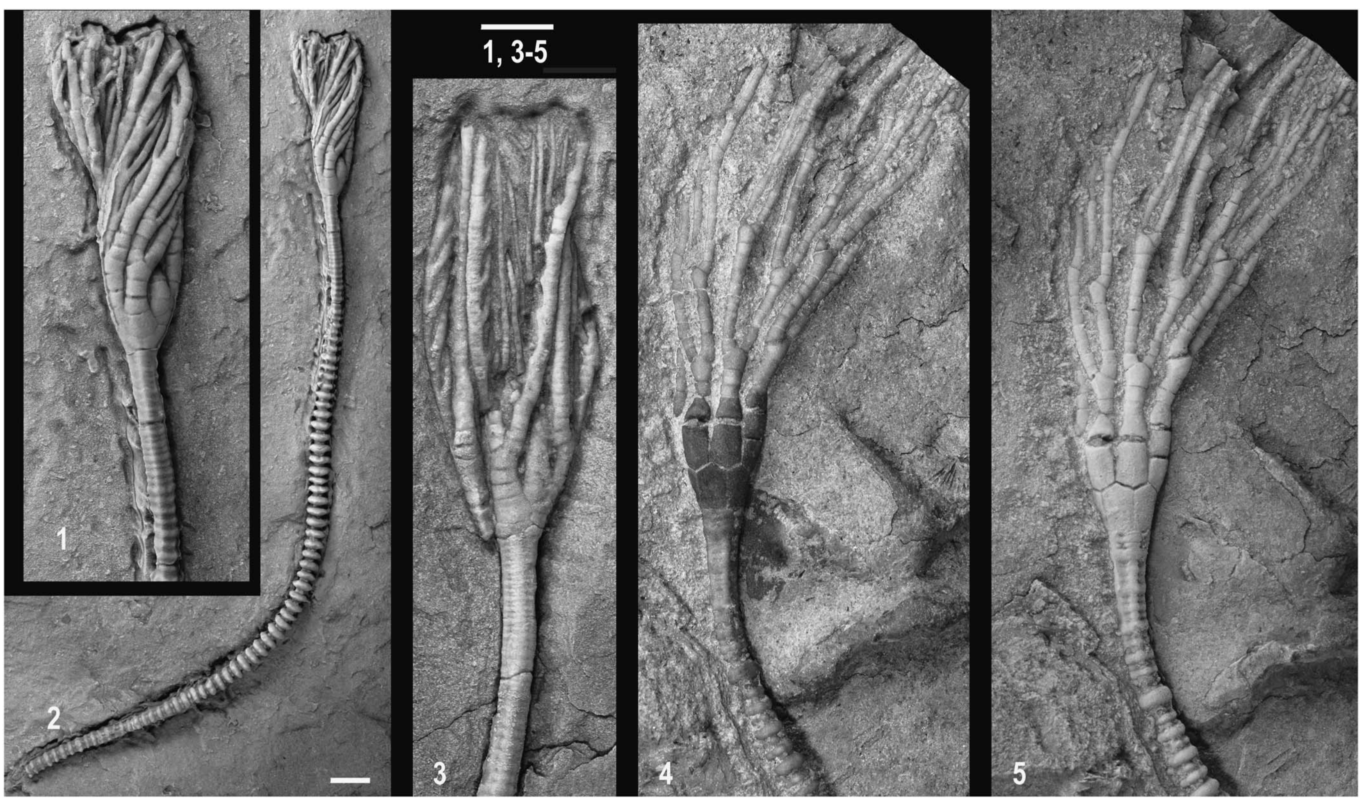

Figure 4. *Daedalocrinus* and *Isotomocrinus*: (**1–3**) *Daedalocrinus bellevillensis* Billings, 1883; (**1**) D-ray view of crown (enlargement of Figure 4.2; compare to Figure 5.1), UMMP 74656; (**2**) D-ray view of specimen (note contrasting morphology of proxistele versus mesistele), UMMP 74656; (**3**) partial crown (note arm branching), UMMP 74655.1; (**4, 5**) *Isotomocrinus tenuis* (Billings, 1857b) lateral view of partial crown and proximal column (note arm branching), UMMP 74658; (**4**) specimen uncoated to illustrate the darker coloration on the aboral cup, proximal brachials, and proximal columnals; (**5**) specimen coated with ammonium chloride prior to photography (note arm branching). Scale bars = 5.0 mm.

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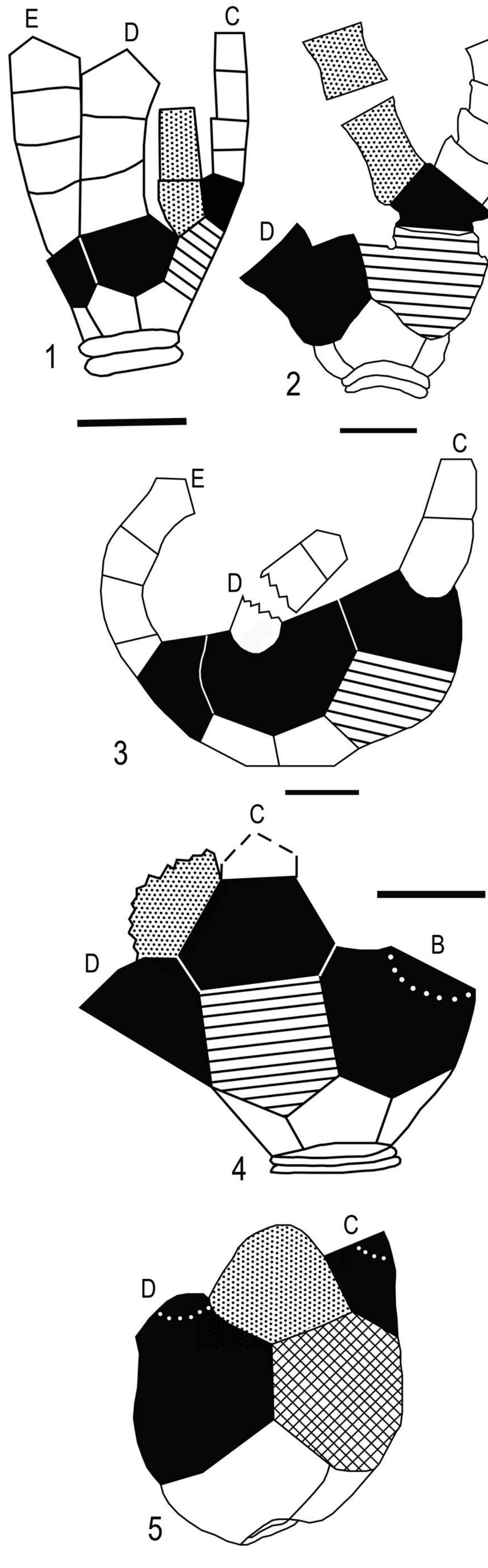

Quarry (Ordovician, Katian). This species also occurs in the Curdsville Member of the Lexington Limestone in Garrard County, Kentucky, USA.

Description.—Crown relatively small; cone slightly expanding. Aboral cup low cone-shaped (Fig. 4.1); width to height ratio ~0.6; plates gently convex; plate sculpture smooth.

Basal circlet ~45% of aboral cup height; basal plates five, pentagonal, approximately as wide as high. Radial circlet ~55% of aboral cup height.

Radial plates five; A and D radial plates simple; B, C, and E radial plates compound. Simple radial plates 1.5 times wider than high. Interradial and superradial plates of approximately same size; interradial plates ~1.6 times wider than high; superradial plates ~2.0 times wider than high (Fig. 4.1). C inferradial plate pentagonal; C superradial plate pentagonal, sutured on distal left shoulder to first anal plate and to C-ray first primibrachial on right shoulder; former suture narrower than latter. Radial facets plenary; topographical details of radial facet unknown.

First anal tetragonal, above aboral cup, supported beneath by C superradial, as wide as high (Fig. 5.1). More distal anal plates above anal X similar to brachials except dimensions approximately as high as wide.

Arms branching once isotomously on third or fourth primibrachial; nonaxillary primibrachials ~1.5 times wider than high. Proximal portion of most proximal primibrachials can be partially fixed to adjacent plates. Above primaxil, arms ramulating with endotomous branching. Ramules branching from arm on every fourth secundibrachial (Fig. 4.3); nonaxillary secundibrachials approximately as high as wide; axillary secundibrachial higher than wide. Ramules long, robust, unbranched; plates of ramules as much as 1.4 times higher than wide.

Column xenomorphic, pentalobate, pentameric. Proxistele columnals homeomorphic, >5 times wider than high, gradually transitioning into mesistele. Mesistele columnals heteromorphic; one internodal between each nodal; nodals ~3.5 times wider than high; internodals approximately four times wider than high (Fig. 4.2). Nodals approximately twice as wide as internodals; mesistele columnals gradually tapering into dististele but retaining organization with nodals separated by one internodal; compared with maximum nodal width in mesistele, nodals at distal end of nearly complete column are half the width. Lumen pentagonal, ~33% of column width; meres aligned with angles of pentagonal lumen. Other details of column facets unknown.

Materials.—*Daedalocrinus kirki* lectotype, USNM S 2141; CMC IP 54045 (2 specimens) 54047, and 54051; GSC 1439a, b; UMMP 74655.1, 74656, and 74657.

Figure 5. Camera lucida drawings of Brechin crinoids: (**1**) *Daedalocrinus bellevillensis* Billings, 1883, D-ray lateral view of partial calyx (compare to Figure 4.1), UMMP 74656; (**2**) *Iocrinus trentonensis* Walcott, 1883, CD interray view of partial crown (compare to Figure 8.2), UMMP 74668.1; (**3**) *Anomalocrinus astrictus* n. sp., D-ray lateral view of partial crown, paratype (compare to Figure 6.3), UMMP 74662; (**4**) *Anomalocrinus astrictus* n. sp., C-ray lateral view of partial crown, holotype (compare to Figure 7), UMMP 74661; (**5**) *Hybocrinus tumidus* Billings, 1857a, CD interray view of aboral cup (compare to Figure 9.2), UMMP 74669. Letters designate Carpenter ray designations; black filling, radial or superradial plate; horizontal ruling, infraradial plate; cross-hatching, radianal plate; stippled, other radial plates. Scale bars = 2.5 mm (**1, 2**); 5.0 (**3 – 5**).

Measurements.—UMMP 74655.1: CrH, 28.0*; ACH, 2.8; CoH, 20.0*. UMMP 74656: CrH, 21.5; ACH, 2.6; maximum ACW, 3.5; CoH, 10.2* (although nearly complete). UMMP 74657: CrH, 11.6*; ACH, 2.2; maximum ACW, 4.1; CoH, 6.0*.

Remarks.—On several specimens, a portion of the calcite skeleton is preserved with a very dark coloration. This most typically occurs on aboral cup plates, but this coloration can extend onto the proximal column and proximal brachials (e.g., UMMP 74657). Whether this represents secondary mineralization or an expression of preserved organic molecules (O'Malley et al., 2013) is not known.

Family Cincinnaticrinidae Warn and Strimple, 1977

Genus *Isotomocrinus* Ulrich, 1925

Type species.—*Isotomocrinus typus* Ulrich, 1925, by monotypy. However, *I. typus* is has been designated a subjective junior synonym of *Heterocrinus tenuis* Billings, 1857b (see Warn and Strimple, 1977).

Other species.—*Isotomocrinus apheles* Ausich, Bolton, and Cummings, 1998 and *I. minutus* Kolata, 1975.

Occurrence.—Ordovician (Darriwilian), Newfoundland, Canada; (Sandbian), Illinois, Iowa, Minnesota, Tennessee, and Wisconsin, USA; and (Katian), New York, USA, and Ontario, Canada.

Remarks.—As with *Daedalocrinus*, Ulrich (1925) proposed a new disparid species as the type species of a new genus; however, that species was subsequently regarded as a junior synonym. Ulrich (1925) designated *Isotomocrinus typus* as the type species of *Isotomocrinus*. Although not recognized as such by Webster and Webster (2013), Warn and Strimple (1977) and Ausich et al. (1998) regarded *I. typus* as a junior subjective synonym of *I. tenuis*, and that opinion is followed here.

Thus, three species of *Isotomocrinus* are considered valid: *I. apheles*, *I. minutus*, and *I. tenuis*. These three species are distinguished on the basis of shape of the aboral cup, number of primibrachials, number of secundibrachials, and arm branching.

Isotomocrinus tenuis (Billings, 1857b)
Figure 4.4, 4.5

1857b *Heterocrinus tenuis* Billings, p. 273.
1868 *Heterocrinus tenuis*; Shumard, p. 377.
1868 *Heterocrinus tenuis*; Bigsby, p. 20.
1886 *Stenocrinus tenuis*; Wachsmuth and Springer, p. 132 (p. 208).
1889 *Heterocrinus tenuis*; Miller, p. 252.
1910 *Heterocrinus tenuis*; Grabau and Shimer, p. 502.
1915 *Heterocrinus tenuis*; Bassler, p. 612.
1925 *Heterocrinus juvenis* Fritz, p. 10, pl. 1, figs. 7, 11, 12, figs. 2, 3 (non Hall, 1866).
1925 *Isotomocrinus typus* Ulrich, p. 86, fig. 5.
1938 *Isotomocrinus typus*; Bassler, p. 119.
1943 *Isotomocrinus typus*; Bassler and Moodey, p. 525.
1944 *Isotomocrinus typus*; Moore and Laudon, p. 149, pl. 52, fig. 11.
1971 *Ectenocrinus* n. sp.; Steele and Sinclair, p. 3, pl. 16, figs. 10, 11.
1973 *Isotomocrinus typus*; Webster, p. 158.
1975 *Isotomocrinus tenuis*; Kolata, p. 26, fig. 8, pl. 4, figs. 9–11.
1977 *Isotomocrinus tenuis*; Warn and Strimple, p. 62, pl. 8, fig. 15.
1978 *Isotomocrinus tenuis*; Brower and Veinus, p. 456, pl. 16, fig. 4.
1986 *Isotomocrinus tenuis*; Webster, p. 180.
1999 *Isotomocrinus typus*; Brett and Taylor, p. 69, fig. 82.
2005 *Isotomocrinus tenuis*; Sloan, p. 153, fig. 4–60.5.
2013 *Isotomocrinus tenuis*; Webster and Webster, p. 1710.
2013 *Isotomocrinus typus*; Webster and Webster, p. 1711.

Holotype.—GSC 1438.

Diagnosis.—Steep-sided medium cone-shaped aboral cup; 4 or 5 primibrachials,; 4–9 secundibrachials; poor isotomous arm branching.

Occurrence.—The original description of *Isotomocrinus tenuis* was based on material from the 'Trenton Limestone' at Ottawa and Montreal, Canada, which are now referred to as the Hull beds. In the Brechin Lagerstätte, this taxon is known from the Bobcaygeon-Verulam contact zone at the Carden Quarry (UMMP 74659) and LaFarge Quarry (UMMP 74658, UMMP 74660) and from the upper Bobcaygeon Formation at the Kirkfield Quarry (Ordovician, Katian). In addition, this taxon has been described from the Buckhorn Member of the Ion Formation in Illinois (Sandbian), the Platteville Group of Illinois (Sandbian), and the Trenton Limestone of New York (Katian), USA.

Description.—Crown medium-sized, constricted at level of proximal primibrachials then an expanding cone thereafter. Aboral cup medium cone-shaped, as high as wide; plates gently convex; plate sculpture smooth (Fig. 4.5).

Basal circlet ~50% of aboral cup height; basal plates five, hexagonal, 1.6 times higher than wide. Radial circlet ~50% of aboral cup height; radial plates five; B and D radial plates simple; A, C, and E radial plates compound; simple radial plates pentagonal, 1.5 times higher than wide; inferradial plates tetragonal, as high as wide; superradial plates pentagonal, slightly higher than wide, extending to approximate level of adjacent radial plates; proximal anal plate on upper left shoulder; C-ray arm on upper right shoulder. Radial facets plenary; details of radial facet topography unknown.

Distal corner of first anal plate supported beneath by C superradial and D radial, pentagonal with uneven sides, approximately as wide as high. More distal anal plates above first anal plate similar to brachials, approximately as high as wide.

Arms branching three times with poor isotomy; ramules absent; first primibrachial trapezoidal, proximal width 1.5 times greater than distal width, height approximately same as proximal width; subsequent primibrachial width 1.25 times wider than high. Axillaries larger than nonaxillary plates. Primaxils from fourth to fifth primibrachial; secundaxil from

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sixth to ninth secundibrachial; tertaxil from ninth to fourteenth tertibrachial. Tertibrachials as high as wide or higher than wide.

Column xenomorphic, pentalobate, pentameric; column index N212. Proxistele with columnals slightly heteromorphic, pentameric or cryptic pentameric; parallel sided; nodals twice as wide as high with ratio higher for internodals; N212 columnal organization present but subtle. Mesistele columnals cryptopentameric or holomeric; nodals approximately two times as wide as high, latus very convex; mesistele first internodals three times wider than high, latus very convex; mesistele tertinternodals 1.6 times as wide as high, straight-sided. Dististele columnals homeomorphic, pentameric. One juvenile specimen with nearly complete column ending in coil; one larger specimen with distal tip abutting against much larger columnal at high angle (thus consistent with but not definitive of distal coil in adult). Aspects of columnal facets unknown.

Materials.—CMC IP 36696, 69219, and 74961; UMMP 74658 – 74660.

Measurements.—UMMP 74658: CrH, 30.0*; ACH, 5.4; ACW, 5.4; CoH, 60.0*. UMMP 74659: CrH, 15.0*; ACH, 2.7; ACW, 3.4*; CoH, 60.0*. UMMP 74660: CrH, 17.0*; ACH, 5.9; ACW, 4.6; CoH, 11.0*.

Remarks.—As with *Daedalocrinus bellevillensis*, the calcite skeleton of *Isotomocrinus tenuis* can be preserved with a very dark coloration (Fig. 4.4). Further, as in *D. bellevillensis*, this occurs most commonly on the aboral cup plates, but on some specimens, the coloration can extend onto the column or onto the proximal brachials.

Isotomocrinus tenuis is a relatively common species from the Brechin Lagerstätte, including both juveniles and adults. The shape of the aboral cup changes through ontogeny with the cup ~1.25 times higher than wide in subadult specimens and more equidimensional in adults.

Family Anomalocrinidae Wachsmuth and Springer, 1886

Remarks.—*Anomalocrinus* is aptly named. The upper Bobcaygeon-lower Verulam interval in Ontario contains numerous specimens of a species that should be assigned to *Anomalocrinus* and *Glaucocrinus falconeri*? Parks and Alcock, 1912, which also could be assignable to *Anomalocrinus*. The original understanding for both *Anomalocrinus* and *Glaucocrinus* Parks and Alcock, 1912 was confused by aberrant specimens. In the holotype of *A. incurvus* Meek and Worthen, 1865, the position of a D radial plate is occupied by two plates separated by a central, vertical suture. Many specimens of *A. incurvus* are known now, and the vertical suture is absent on other specimens, making the holotype presumably an aberrant morphology. The holotype of *G. falconeri* has only three free arms. The C and E radial plates lack an arm (Guensburg, 1992). As suggested by Guensburg (1992), the holotype of *G. falconeri* is undoubtedly also an aberrant specimen. Guensburg (1992) clarified the morphology of *G. falconeri*, including the presence of only three arms; and otherwise demonstrated that the reconstruction by Parks and Alcock (1912) and by Moore and Lane (1978b) did not represent the morphology of this taxon. Guensburg (1992) also demonstrated that the arms are only partially preserved, and the aboral cup is compressed. Guensburg acknowledged that *Glaucocrinus* could be a junior synonym of *Anomalocrinus*, but with only the holotype available for study, Guensburg (1992, p. 6) concluded "I prefer to retain the status quo for the present; however, *Glaucocrinus* and *Anomalocrinus* are clearly closely related taxa."

Comparison of the holotype of *Glaucocrinus falconeri* (see Guensburg, 1992, fig. 2) with the new *Anomalocrinus* material from the Brechin Lagerstätte supports the suggestion of Guensburg (1992) that *Glaucocrinus* is probably a junior synonym of *Anomalocrinus* and that the holotype and only known specimen of *G. falconeri* is an aberrant specimen. However, critical features needed to diagnose the species of *Anomalocrinus* (shape of the aboral cup, nature of brachials, and arm branching in the C and E rays) are not preserved on the holotype of *G. falconeri*, precluding comparison with other species of *Anomalocrinus*. Therefore, both *G. falconeri* and its monospecific genus *Glaucocrinus* are unrecognizable because of poor preservation and the fact that the holotype and only specimen is an aberrant individual. Thus, we designate *Glaucocrinus* and *G. falconeri* as nomina dubia. With the reassignment of *Geraocrinus* Ulrich, 1925 to the Columbicrinidae (see Ausich, 1998), and the designation of *Glaucocrinus* as a nomen dubium, the Anomalocrinidae is monogeneric.

Genus *Anomalocrinus* Meek and Worthen, 1865

Type species.—*Heterocrinus?* (*Anomalocrinus*) *incurvus* Meek and Worthen, 1865, by monotypy.

Other species.—?*A. antiquus* Guensburg, 1984; *A. caponiformis* (Lyon, 1869); *A. astrictus* n. sp.

Occurrence.—Ordovician (questionably Sandbian), Tennessee, USA; (Katian), Indiana, Ohio, and Tennessee, USA, and Ontario, Canada.

Remarks.—Although beyond the scope of the present investigation, it should be noted that the previously named species of *Anomalocrinus* are in need of reevaluation. Specimens of *Anomalocrinus* are relatively large with relatively thin calyx plates; thus, specimens are easily compacted and disarticulated. This could explain the relative paucity of *Anomalocrinus* crowns preserved relative to, at least locally, the abundance of the distinctive *Anomalocrinus* holdfasts (Brett et al., 2008). Although specimens are available in museums, very few crowns of *A. incurvus* have been illustrated previously. It is probable that the holotype of *A. incurvus* is, as noted above, an aberrant specimen, and *A. caponiformis* is only known from a theca. Further, ?*A. antiquus* is a very small specimen and is known only from the aboral cup and proximalmost arms.

As presently understood, species of *Anomalocrinus* are diagnosed by the following characters: attitude of the radial circlet, the general character of the arms, character of the C-ray and E-ray primibrachials, shape of brachials, position of the primaxil, position of secundaxil, and arm branching. *Anomalocrinus astrictus* n. sp. has a more vertically directed radial circlet; brachials higher than wide, C- and E-ray primibrachials much larger than those in other rays; typically first primibrachial axillary in A, B, and D rays; third to fourth primibrachial axillary in C and E rays; the second to fourth secundibrachial is axillary, and as many as six bifurcations in an arm. In contrast, *A. incurvus* has an outflaring radial circlet; C- and E-ray primibrachials approximately the same size as those in other rays; the first or second primibrachial axillary in A, B, D, and E rays, more primibrachials in C ray; third or sixth secundibrachial axillary; and at least four bifurcations in an arm. ?*Anomalocrinus antiquus* has an more vertically oriented radial circlet, one partial arm and primibrachials in two other rays preserved, brachials higher than wide, the first primibrachial is axillary, and an axillary in the secundibrachitaxis (if present) higher than the third secundibrachial.

Anomalocrinus astrictus new species
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Figures 5.3, 5.4, 6, 7

Type specimens.—Holotype, UMMP 74661; paratypes, UMMP 74662 and 74663.

Diagnosis.—*Anomalocrinus* with radial circlet more vertically oriented, angustary radial facets (except C ray), brachials higher than wide, the first or the fourth primibrachial axillary (most commonly first), second to fourth secundibrachial axillary, and as many as six bifurcations in an arm.

Occurrence.—This new species is known only from the Brechin Lagerstätte in the Bobcaygeon-Verulam contact zone at the Carden Quarry (UMMP 74662) and the LaFarge Quarry (UMMP 74663) (Ordovician; Katian).

Description.—Crown medium-sized, subcylindrical. Aboral cup low bowl shaped, ~1.5 times wider than high; plates gently convex, plate sculpture smooth (Fig. 6.1).

Basal circlet ~35% of aboral cup height; basal plates five, pentagonal, ~1.5 times wider than high. Radial circlet more vertically directed, ~65% of aboral cup height; radial plates five, A, B, and D radial plates simple, 2.0 times wider than high; C and E radial plates compound (Figs. 5.3, 6.3, 7); infer- and superradial plates together larger than one simple radial plate; C infer- and superradial plates narrower and more equidimensional than simple radial plates; C inferradial plate pentagonal, as wide as high; C superradial plate octagonal, mostly above the distal extent of other radial plates, tapering distally, maximum width greater than height. A, B, D, and E radial facets angustary to peneplenary, ~60–80% of distal radial plate width; C radial facet plenary (Fig. 5.4), details of facet surface unknown.

First anal plate above aboral cup, sutured beneath to upper shoulders of C superradial and D radial plates (Fig. 7).

Arms branching isotomously as many as six times. Nonaxillary brachials rectilinear uniserial, convex with straight or concave sides; progressively higher-order brachitaxes with more exaggerated concave sides (Fig. 6.1); all axillaries with concave sides (except for some first primibrachials that are axillary, very small, sublenticular, and 1.25 times wider than high). A, B, and D rays typically with first primibrachial axillary; C and E rays with three or four primibrachials that are much larger than those of other rays. Nonaxillary brachials becoming progressively higher than wide from proximal to distal. Beginning in secundibrachitaxis, gracile ramules branching at irregular intervals (ramules from either every successive brachial or separated by nonaxillary brachials). Ramulars up to four times higher than wide, rectilinear uniserial with concave sides.

Column heteromorphic (Fig. 6.2), subcircular to multilobate. Periphery of many internodals with a beaded appearance. Proxistele columnals up to 22 times wider than high; mesistele columnals organized as N3231323, ranging from ~30 to 7.5 times wider than high.

Etymology.—The new species name is derived from *astrictus* (L.) meaning drawn, together, tight, narrow, close; and it refers to the medial constriction of the width of the brachials.

Materials.—UMMP 74661–74663.

Measurements.—UMMP 74661, holotype: CrH, 61.1*; ACH, 8.8; ACW, 17.6; CoH, 18.0*. UMMP 74662, paratype: CrH, 56.0; ACH, 12.0; ACW, 21.2; CoH, 80.5*. UMMP 74663, paratype: CrH, 58.0*; ACH, 8.0*; ACW, 20*; CoH, 90*.

Remarks.—See species comparisons in remarks for genus.

Order Calceocrinida Ausich, 1998
Family Calceocrinidae Meek and Worthen, 1869

Genus *Cremacrinus* Ulrich, 1886

Type species.—*Cremacrinus punctatus* Ulrich, 1886.

Other species.—*Cremacrinus arctus* Sardeson, 1928; *C. articulosus* (Billings, 1859); *C. billingsianus* (Ringueberg, 1889); *C. crossmani* Brower and Strimple, 1983; *C. decatur* Springer, 1926; *C. drummuckensis* (Ramsbottom, 1961); *C. forrestonensis* (Kolata, 1975); *C. furcillatus* (Billings, 1887); *C. gerki* Brower and Strimple, 1983; *C. guttenbergensis* Kolata, 1975; *C. inaequalis* (Billings, 1859); *C. kentuckiensis* (Miller and Gurley, 1894); ?*C. latus* (Brower and Veinus, 1974); *C. lucifer* Bolton, 1970; *C. ramifer* (Brower, 1977); *C. rugosus* (Billings, 1887); *C. tubuliferus* Springer, 1926; and *C. ulrichi* Springer, 1926.

Occurrence.—Ordovician (Sandbian), Illinois, Iowa, Minnesota, Oklahoma, and Wisconsin, USA; Katian, Illinois, Iowa, Kentucky, Minnesota, Tennessee, and Wisconsin, USA, Ontario, Canada, and Scotland; Silurian (Ludlow and Pridoli), Tennessee, USA.

Remarks.—Six species of *Cremacrinus* have been reported from the Ordovician in Ontario and Quebec: *C. articulosus*, *C. billingsianus*, *C. furcillatus*, C. *inaequalis*, *C. lucifer*, and *C. rugosus*. Wilson (1946) noted that both *C. furcillatus* and *C. rugosus* were known from single specimens that were lost. In addition, many additional species are known from the United States (Webster and Webster, 2013). The presence or absence of three characters can be used to quickly subdivide *Cremacrinus* into groups: (1) E-ray arm divided or atomous;

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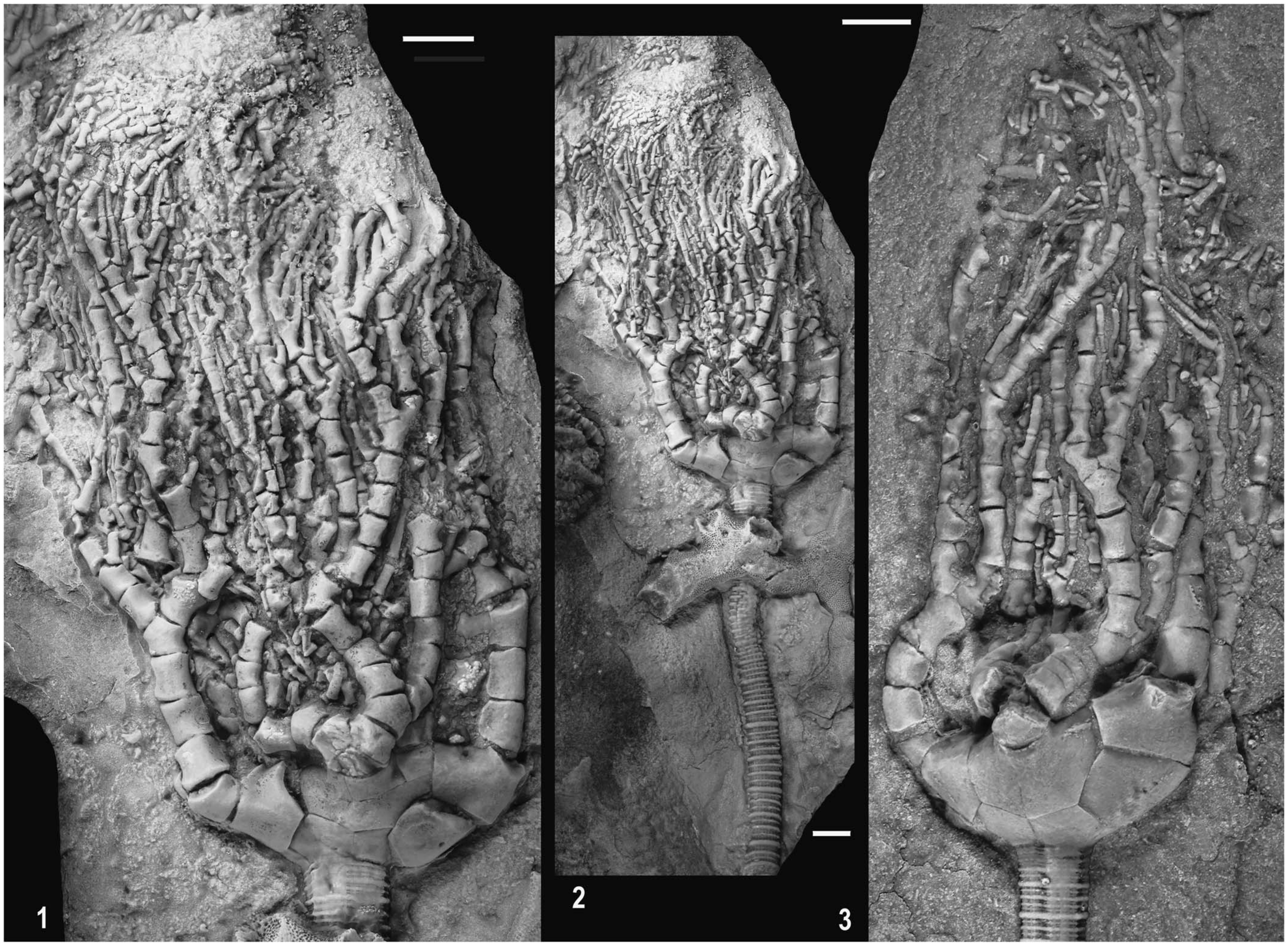

Figure 6. *Anomalocrinus astrictus* n. sp., paratypes: (**1–2**) A-ray lateral view of partially disarticulated crown and column, UMMP 74663; (**1**) note arm branching and brachial morphology, enlargement of Figure 6.2; (**2**) crown with column; (**3**) D-ray lateral view of partially disarticulated crown with column, note compound (compare to Figure 5.3), UMMP 74662. Scale bars = 5.0 mm.

(2) brachials rectilinear uniserial or cuneate uniserial; and (3) brachial plates wider than high or higher than wide.

As discussed below, two species of *Cremacrinus* occur in the Brechin fauna, one with the E-ray arm undivided and rectilinear uniserial brachials that are wider than high and the other with E-ray arm undivided and cuneate uniserial brachials that are higher than wide. These are regarded below as *C. inaequalis* and *C. guttenbergensis* Kolata, 1975, respectively.

Cremacrinus guttenbergensis Kolata, 1975
Figure 8.4, 8.5

1975 *Cremacrinus guttenbergensis* Kolata, p. 23, fig. 6, pl. 3, figs. 10, 14.
1982 *Cremacrinus guttenbergensis*; Brower, p. 92.
1983 *Cremacrinus guttenbergensis*; Brower and Strimple, p. 1277, figs. 10a–c, 11a–c.
1986 *Cremacrinus guttenbergensis*; Webster, p. 105.
1988 *Cremacrinus guttenbergensis*; Brower, p. 919.
1988 *Cremacrinus guttenbergensis*; Webster, p. 60.
1993 *Cremacrinus guttenbergensis*; Webster, p. 41.
2013 *Cremacrinus guttenbergensis*; Webster and Webster, p. 1121.

Holotype.—BMNH PK-45.

Diagnosis.—*Cremacrinus* with coarsely pitted aboral cup sculpture; aboral cup wider than high; aboral cup plates not swollen; axil arms two; axillaries not swollen; arms robust; brachials cuneate or rectilinear uniserial and higher than wide; B arm smaller than A and D arms; E-ray arm unbranched.

Occurrence.—This taxon was founded on specimens from the Guttenberg Formation (Galena Group) in Illinois and Wisconsin (Katian), USA. Subsequently it has been recovered from the Mortimer and Sherwood members of the Dunleith Formation (Sandbian) of Illinois, Iowa, and Minnesota, and the Trenton Formation in New York (Katian), USA. In the Brechin Lagerstätte, this species of *Cremacrinus* is known from the Bobcaygeon-Verulam contact zone at the Carden Quarry (UMMP 74664, UMMP 74665.1) and from the upper Bobcaygeon Formation at the Kirkfield Quarry and Tomlinson Quarry (Ordovician, Katian).

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Figure 7. *Anomalocrinus astrictus* n. sp., holotype, C-ray lateral view of partial crown (note large brachials in the C-ray arm); calyx sculpture is smooth and pitting on calyx plates on this specimen is a preservational artifact (compare to Figure 5.4), UMMP 74661. Scale bar = 5.0 mm.

Description.—Crown without perfect bilateral symmetry, probably pendant on column. Aboral cup small, adorally-aborally compressed; plate sculpture coarsely pitted; sutures impressed (Fig. 8.5).

Basal plates four, all in column concavity, all part of distal margin of basal circlet. Radial circlet almost twice as wide as high, wider proximally, tapering distally (Fig. 8.5); trapezoidal and slightly indented along line between proximal edge of A and D radial facets; ligament pit divided. A and D radial plates occupying majority of radial circlet. E-ray inferradial and superradial with narrow sutural contact; E superradial trapezoidal; E inferradial trapezoidal, occupying ~20% of radial-basal articulation; E superradial occupying ~55% of the distal aboral cup margin. Distal facet of A and D radials supporting a lateral arm. Other aspects of radial and anal plates unknown, including verification that B arm is present.

Four arms presumably present. Arms slender with aborally convex brachials; brachials rectilinear uniserial or cuneate uniserial, higher than wide, yielding arms with zig-zag appearance. Main axil with nonaxillary brachials; divisions isotomous. E-ray arm unbranched; E-ray brachials higher than wide, rectilinear uniserial (Fig. 8.4). Main axils weakly developed; two axillaries present, each separated by one nonaxillary brachial. Lateral arms apparently with normal bilateral heterotomy. Primaxil arm bifurcating at least through epsilon axillary with two (proximally) or four (distally) nonaxillary brachials before each bifurcation; three divisions preserved on betaaxil arm with three and five nonaxillary brachials before each bifurcation; beta ramules not visible. Other details of arms unknown.

Column homeomorphic; proxistele with very thin columnals with wavy or straight sutures. Beneath aboral cup proxistele columnals approximately six times wider than high and wedge shaped. Mesistele and dististele columnals three times wider than high. Holdfast an irregular, subovate mass of stereom cemented to crinoid pluricolumnal. Holdfast classified as simple, discoidal, cemented type (Fig. 8.4).

Materials.—CMC IP 366334 (3 specimens); UMMP 74664 and 74665.1.

Measurements.—UMMP 74664: CrH, 30.0*; ACH, 5.0; proximal, ACW, 7.0; CoH, 24.0. UMMP 74665.1: CrH, 30.0; ACH, 4.5; proximal ACW, 5.1; CoH, 19.5*.

Remarks.—See remarks under genus.

Cremacrinus inaequalis (Billings, 1859)
Figure 9.4, 9.5

1859 *Heterocrinus inaequalis* Billings, p. 51, pl. 4, fig. 7a.
1868 *Heterocrinus inaequalis*; Shumard, p. 377.
1868 *Heterocrinus inaequalis*; Bigsby, p. 20.
1886 *Cremacrinus inaequalis*; Ulrich, p. 113.
1889 *Calceocrinus inaequalis*; Miller, p. 230.
1889 *Castocrinus inaequalis*; Ringueberg, p. 395, pl. 10, fig. 5.
1915 *Cremacrinus inaequalis*; Bassler, p. 289.
1943 *Cremacrinus inaequalis*; Bassler and Moodey, p. 376.
1946 *Cremacrinus inaequalis*; Wilson, p. 35, pl. 5, fig. 4.
1962 *Cremacrinus inaequalis*; Moore, p. 21.
1973 *Cremacrinus inaequalis*; Webster, p. 86.
1982 *Cremacrinus inaequalis*; Brower, p. 93.
1988 *Cremacrinus inaequalis*; Webster, p. 60.

Holotype.—GSC 1444.

Diagnosis.—*Cremacrinus* with smooth aboral cup sculpture; aboral cup wider than high; aboral cup plates not swollen; axil arms two; axillaries not swollen; arms slender; brachials rectilinear uniserial, wider than high; E-ray arm unbranched.

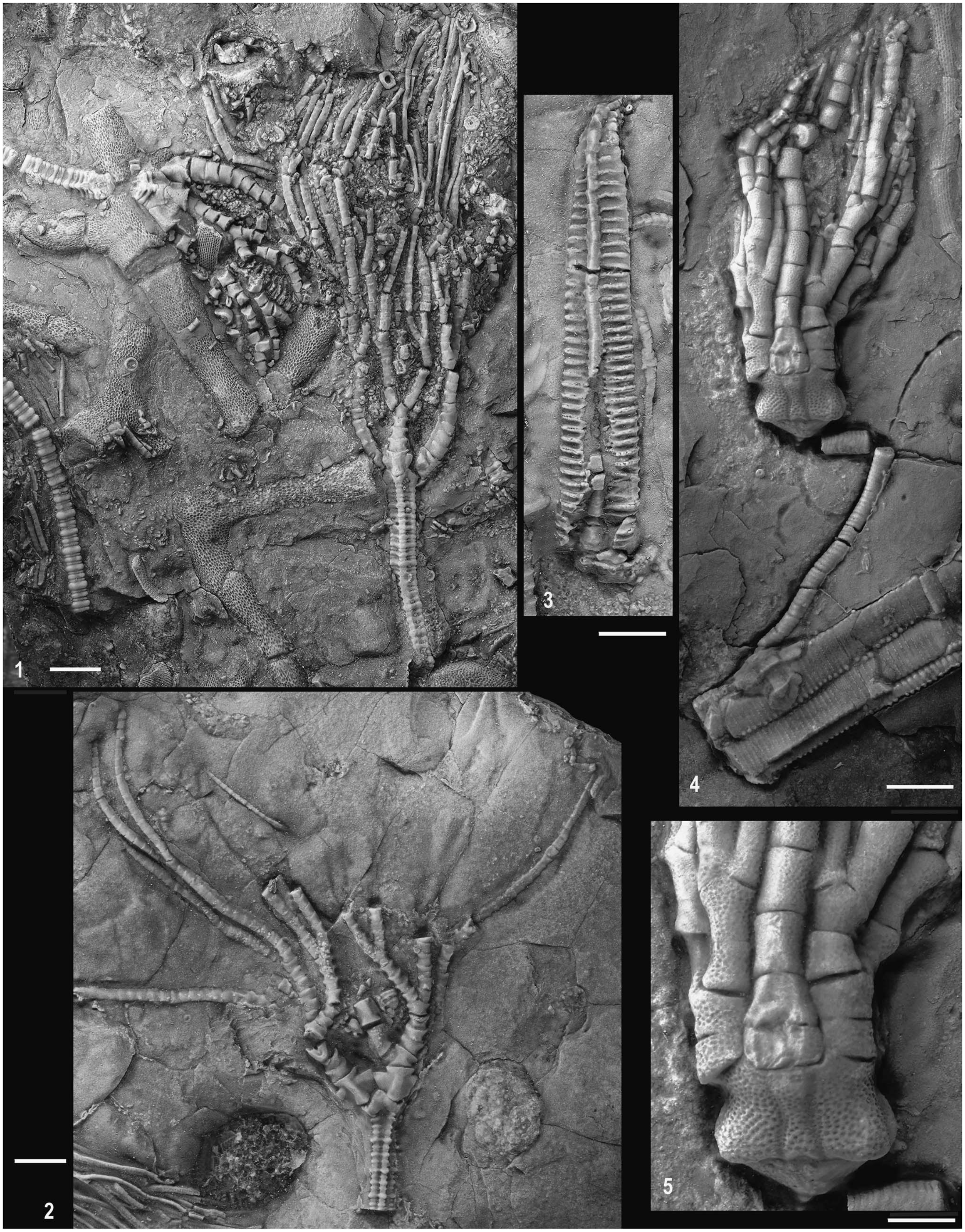

Figure 8. *Iocrinus trentonensis* Walcott, 1883 and *Cremacrinus guttenbergensis* Kolata, 1975: (**1–3**) *Iocrinus trentonensis*; (**1**) two partial specimens (note arm branching on the larger specimen and aboral cup shape on the smaller specimen), UMMP 74667.1–74667.2; (**2**) CD interray view of partial crown illustrating the compound radial plate in the C ray (compare to Figure 5.2), UMMP 74668.1; (**3**) isolated anal sac with the typical *Iocrinus* anal sac morphology, UMMP 74668.2; (**4–5**) E-ray view of a nearly compete specimen of *Cremacrinus guttenbergensis*, UMMP 74664; (**4**) note complete (if partially disarticulated) column and encrusting holdfast, first few brachials of E ray damaged prior to collection; (**5**) enlargement of aboral cup, note pitted plate sculpture. Scale bars = 2.5 mm (**5**); 5 mm (remaining).

Occurrence.—*Cremacrinus inaequalis* was originally described from the Cobourg beds (now Lindsay Formation) at Ottawa, Canada (Ordovician, Katian), and has also been reported from the Sandbian-Katian Prosser Limestone of Minnesota and Wisconsin, USA. In the Brechin Lagerstätte, it is known from the Bobcaygeon-Verulam contact zone at the Carden Quarry (UMMP 74665) and from the upper Bobcaygeon Formation at the Kirkfield Quarry (Ordovician, Katian).

Description.—Crown without perfect bilateral symmetry, pendant on column. Aboral cup medium-sized, adorally-aborally compressed; plate sculpture smooth; sutures impressed (Fig. 9.4).

Basal plates four, all in column concavity, all part of distal margin of basal circlet. Radial circlet wider than high, wider proximally, tapering distally (Fig. 9.5); condition of ligament pit unknown. A and D radial plates occupying majority of radial circlet. E-ray inferradial and superradial with wide sutural contact; E superradial trapezoidal; E inferradial pseudo-rectangular, occupying ~25% of radial-basal articulation; E superradial occupying ~50% of distal aboral cup margin (Fig. 9.5). Distal facet of A, B, and D radials support a lateral arm. Other aspects of radial and anal plates unknown.

Four arms presumably present. Arms moderately robust with aborally convex brachials; brachials rectilinear uniserial, wider than high. Main axil with nonaxillary brachials; first division isotomous; second division heterotomous. E-ray arm unbranched; E-ray brachials wider than high (Fig. 9.4). Main axils weakly developed; two axillaries present, each separated by one nonaxillary brachial. Lateral arms apparently with normal bilateral heterotomy. Primaxil arm bifurcating at least through epsilon axillary with two to five nonaxillary brachials before each bifurcation; two divisions preserved on betaaxil arm with three and six (proximal/distal) nonaxillary brachials before each bifurcation; beta ramules not visible. B arm with one nonaxillary before first bifurcation and four before second bifurcation; further aspects of B arm covered. Other details of arms unknown.

Column apparently homeomorphic, although columnals very thin near aboral cup. Beneath aboral cup columnals approximately six times wider than high and wedge shaped.

Materials.—CMC IP 54773; UMMP 74666.

Measurements.—UMMP 74666: CrH, 40.0*; ACH, 6.8; proximal ACW, 8.7; CoH, 7.4*.

Remarks.—See remarks under genus.

Order Myelodactylida Ausich, 1998
Family Iocrinidae Moore and Laudon, 1943

Genus *Iocrinus* Hall, 1866

Type species.—*Heterocrinus* (*Iocrinus*) *polyxo* Hall, 1866 = *H. subcrassus* Meek and Worthen, 1865.

Other species.—*Iocrinus africanus* Zamora, Rahman, and Ausich, 2015; *I. crassus* (Meek and Worthen, 1865); *I. llandegleyi* Botting, 2003; *I. pauli* Donovan and Gale, 1989; *I. subcrassus torontoensis* Fritz, 1925 (herein regarded as a synonym of *I. subcrassus*); and *I. trentonensis* Walcott, 1883.

Occurrence.—Ordovician (latest Dapingian to early Darriwilian), Oman; (Darriwilian) England, Morocco, and Wales; (Katian) Illinois, Indiana, Iowa, Kentucky, New York, and Ohio, USA, and Ontario, Canada.

Remarks.—Four species (plus one subspecies) of *Iocrinus* have been described from Katian strata of eastern North America. These include the type species, *I. subcrassus*, from the Greater Cincinnati region, New York, USA and Ontario, Canada; *I. crassus* from the Maquoketa Formation of Illinois, USA; and *I. trentonensis* from the Spillway Member of the Rust Formation in New York, USA. In addition, *I. subcrassus torontoensis* has been named.

As discussed by Wilson (1946), Kelly (1978), and Brower (2008), *Iocrinus similis* is known only known the holotype (GSC 1428), which is a damaged specimen lacking key features of the aboral cup. Further, the specimen is most likely a teratological specimen with an extra plate inserted between the C-ray infer- and superradial plates (Kelly, 1978). Thus, we designate, herein, *I. similis* as a nomen dubium.

Fritz (1925, p. 13) named *Iocrinus subcrassus torontoensis* (holotype ROM 245) based on two specimens in which the C-ray arm has five primibrachials rather than three. As noted by Brower (2008, p. 59), the number of primibrachials of *I. subcrassus* ranges from three to five with a mean of 4.13. Therefore, because the diagnostic characteristic of *I. subcrassus torontoensis* falls within the recognized range of this feature for *I. subcrassus* populations, designation of a subspecies is deemed unwarranted, and *I. subcrassus torontoensis* is designated, herein, a junior synonym of *I. subcrassus*.

In summary, three valid Katian species are now recognized from eastern North America. These three species can be differentiated as follows: *Iocrinus subcrassus* is medium-sized; proximal aboral cup width to aboral cup height 1.17; distal aboral cup width to aboral cup height 2.12 (means from Brower, 2008); first primibrachial approximately two times wider than high; 5–13 tertibrachials (mean 7.99, from Brower, 2008); typically four (range three to eight) in-line bifurcations within a ray; brachials with distal flanges only proximally. *Iocrinus crassus* is large; proximal aboral cup width to aboral cup height 0.9; distal aboral cup width to aboral cup height 1.8 (means from Brower, 2008); first primibrachial approximately two times wider than high; four to eight tertibrachials; as many as seven in-line bifurcations within a ray; brachials without distal flanges. *Iocrinus trentonensis* is small; proximal aboral cup width to aboral cup height 0.697; distal aboral cup width to aboral cup height 1.79 (means from Brower, 2008); first primibrachial ~1.4–2 times wider than high; 5–13 tertibrachials (mean 7.99, from Brower, 2008); three to five in-line bifurcations within a ray; brachials with distal flanges throughout arms.

Iocrinus trentonensis Walcott, 1883
Figures 5.2, 8.1–8.3

1883 *Iocrinus trentonensis* Walcott, 1883, p. 4, pl. 17, figs. 7, 8.
1884 *Iocrinus trentonensis*; Walcott, p. 210, pls. 17, 18.

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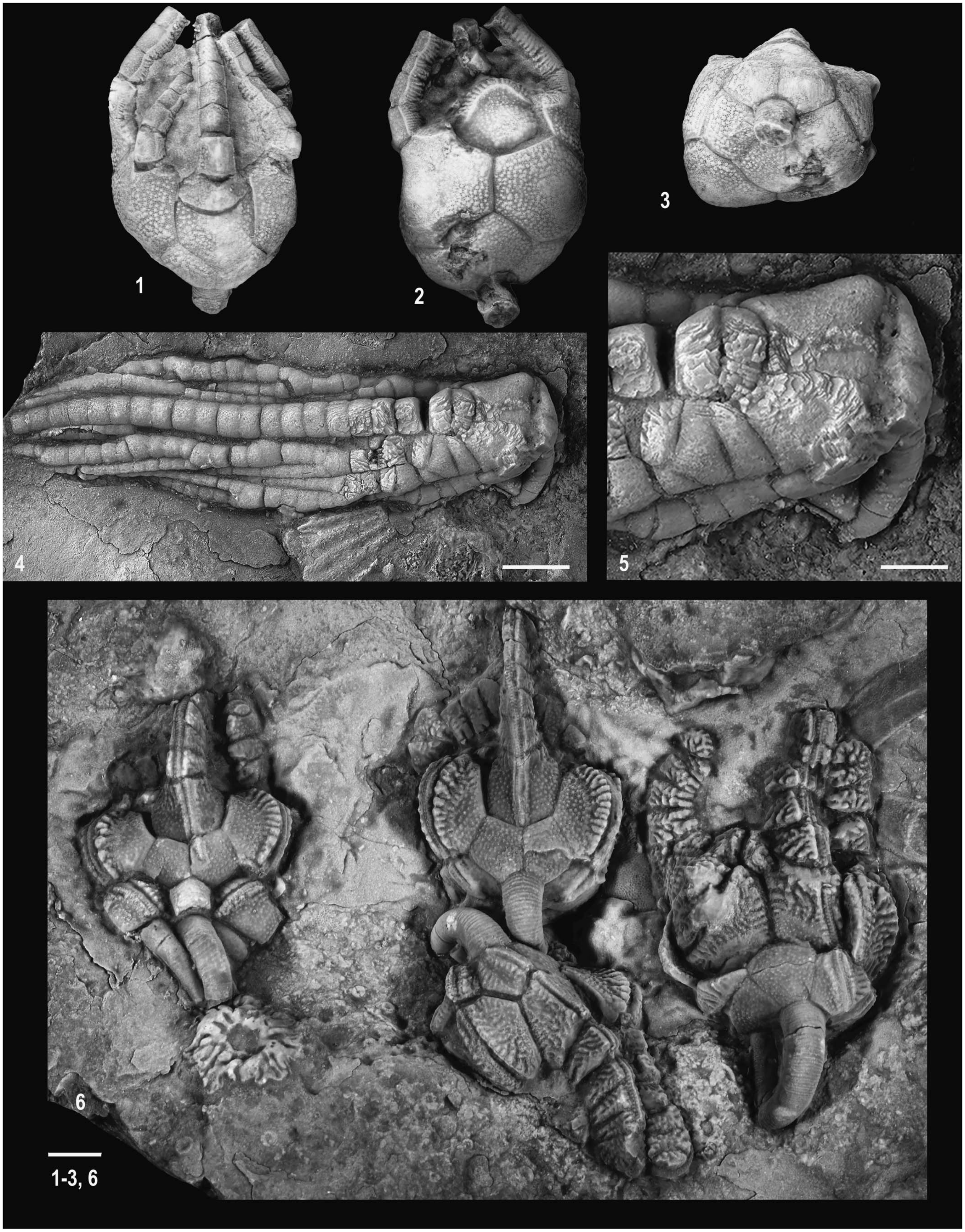

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1889 *Iocrinus trentonensis*; Miller, p. 257.
1915 *Iocrinus trentonensis*; Bassler, p. 668.
1943 *Iocrinus trentonensis*; Bassler and Moodey, p. 525.
1999 *Iocrinus trentonensis*; Brett and Taylor, p. 65, fig. 74.
2007 *Iocrinus trentonensis*; Brower, p. 1285, fig. 2.10–2.12.
2008 *Iocrinus trentonensis*; Brower, p. 59, figs. 2–5.
2011 *Iocrinus trentonensis*; Brower, p. 270, fig. 2.1–2.2.
2013 *Iocrinus trentonensis*; Webster and Webster, p. 1707.

Type specimens.—Lectotype, MCZ 106417; paralectotype, MCZ 113426 (see Brower, 2008).

Diagnosis.—Relatively small species with aboral cup distal width to height ratio much more than twice that of aboral cup proximal width versus height; basal plate height ~50% of radial plate height; radial plate height and width approximately equal; transverse ribbing between adjacent aboral cup plates; first primibrachial width versus height 1.5 or less; four to six primibrachials; six to nine secundibrachials; six to fifteen tertibrachials; three to five in-line bifurcations per ray; brachials with distal flanges through most of arm height; anal sac robust.

Occurrence.—*Iocrinus trentonensis* was originally described from the Trenton Limestone of New York, USA. It is now recognized from the Spillway Member, Rust Limestone (Katian) in New York and the Brechin Lagerstätte from the Bobcaygeon-Verulam contact zone at the Carden Quarry (UMMP 74667.1) and from the lower Verulam Formation at the James Dick Quarry (UMMP 74668) (Ordovician, Katian).

Description.—Crown medium-sized, expanding cone-shaped. Aboral cup flat cone-shaped; height to width ratio ~4.0; plates sharply convex; plate sculpture smooth (Fig. 8.2).

Basal circlet ~33% of aboral cup height; basal plates five, hexagonal, 3.0 times higher than wide; basal-basal plate sutures depressed. Radial circlet ~67% of aboral cup height; radial plates five; A, B, D, and E radial plates simple. Simple radial plates ranging from as wide as high to 1.4 times wider than high, very convex with broad ridge connecting adjacent radial plates, deeply concave at radial-radial-basal plate triple junction. C radial plate compound; C inferradial pentagonal, 1.5 times wider than high, same sculpture as simple radial plates; C superradial plate above aboral cup, subpentagonal, 1.7 times wider than high, constricted medially a short distance above proximal suture; anal X supported on left with slightly shorter suture than C-ray arm to right (Figs. 5.2, 8.2). Radial facets peneplenary, occupying 75% of distal width of radial facet; facet topography unknown.

First anal plate above aboral cup, supported beneath by only C superradial, hexagonal, slightly contorted, ~1.2 times higher than wide. Second anal plate quadrangular, approximately as high as wide. Based on anal sac plates preserved within crown and isolated, intact anal sac preserved adjacent to *Iocrinus* crowns; anal sac large, cylindrical, comprised of two columns of robust plates as high as wide (one in CD-interray orientation, one in A-ray orientation); two columns connected laterally by concave, very wide plates with plicated, depressed sutures; sutures covered by small plates (Fig. 8.3).

Arms branching four or five times isotomously (Fig. 8.1); nonramulate; first primibrachial quadrangular, ~1.5 times wider than high; fourth primibrachial axillary in all rays. Secundibrachials and higher quadrangular, as high as wide; fifth to seventh secundibrachial axillary.

Column pentalobate, heteromorphic, holomeric; largest columnals four times wider than high; latus convex (Fig. 8.1). Lumen circular, ~15% of columnal width; columnal facets unknown.

Materials.—UMMP 74667.1, 74667.2, 74668.1, and 74668.2.

Measurements.—UMMP 74667.1: CrH, 48.0; ACH, 3.1; distal ACW, 6.8; CoH 42.8*. UMMP 74668.1: ACH, 4.7; distal ACW, 7.4; CoH, 26.0*. UMMP 74668.2: CrH, 49.2.; ACH, 5.0; distal ACW, 7.7; CoH 50.0.

Remarks.—As noted above, *Iocrinus trentonensis* can be readily differentiated from the other two North American species of *Iocrinus*. *Iocrinus trentonensis* is closest to *I. subcrassus* and might be a paedomorphic derivative of *I. subcrassus*, with smaller size, fewer brachial plates within brachitaxes, wider radial plates, a wider aboral cup, and flanges throughout the height of the arms. Of the two species, *I. subcrassus* is the most widespread geographically of the two species, although both occur in Katian strata of Ontario, Canada. Only *I. trentonensis* is known from the Brechin fauna.

Although this taxon is recognized by relatively small specimens, *Iocrinus trentonensis* is regarded as an adult based on the morphology of the brachial plates, which are wider than high rather than higher than wide.

Parvclass Cladida Moore and Laudon, 1943
Superorder Porocrinoidea Wright, 2017
Order Hybocrinida Jaekel, 1918
Family Hybocrinidae Zittel, 1879

Genus *Hybocrinus* Billings, 1857a

Type species.—*Hybocrinus conicus* Billings, 1857a, by subsequent designation.

Other species.—*Hybocrinus bilateralis* Guensburg, 1984; *H. crinerensis* Strimple and Watkins, 1949; *H. nitidus* Sinclair, 1945; *H. perperamnominatus* Brower and Veinus, 1974;

Figure 9. Hybocrinidae and Calceocrinidae: (**1–3**) *Hybocrinus tumidus* Billings, 1857a, UMMP 74669; (**1**) A-ray view of partial crown (note robust, uniserial brachials of atomous arms; note radial plate is broken with an arcuate fracture); (**2**) CD interray view of partial crown (note the prominent ridges along the convex distal surface of the first anal plate and the prominent grooves on the sides of brachials; compare to Figure 5.5); (**3**) basal view of calyx; (**4, 5**) slightly askew E-ray view of crown and column of *Cremacrinus inaequalis* Billings, 1859 (note damage on some calyx and proximal brachials prior to collection), UMMP 74666; (**4**) entire crown; (**5**) enlargement of aboral cup (note short length of column tucked beneath the aboral cup); (**6**) four partially compressed adult individuals of *Hybocystites problematicus* Wetherby, 1880 (note prominent sculpture on plates, prominent ridges on brachials and along recumbent ambulacra, and proximal extensions of recumbent ambulacra), UMMP 74670.1–74670.4. Scale bars 2.5 mm (**5**); 5.0 mm (remaining).

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H. pristinus Billings, 1858; *H. punctatocristatus* Brower and Veinus, 1974; *H. punctatus* (Miller and Gurley, 1895); and *H. tumidus* Billings, 1857a.

Occurrence.—Ordovician (Sandbian), Illinois, Iowa, Kentucky, Oklahoma, Minnesota, Tennessee, Virginia, and Wisconsin, USA; (Katian), Ontario, Canada.

Remarks.—Billings (1857a) assigned two new species (*Hybocrinus conicus* and *H. tumidus*) from the Upper Ordovician to his new genus *Hybocrinus*; in 1858, he described a third species, *H. pristinus* (see Billings, 1958). These are the three species of *Hybocrinus* known from Ontario, Canada. As noted below, only *H. tumidus* is recognized from the Brechin fauna, and *H. pristinus* is considered a junior synonym of *H. tumidus*.

Species characters in *Hybocrinus* are: overall calyx symmetry about the oral-aboral axis, calyx outline in oral view, calyx plate sculpture, summit attitude, basal plate size, anal X shape, nature of the distal margin of the first anal plate, presence or absence of a stout A-ray arm, and position of column facet.

Hybocrinus tumidus Billings, 1857
Figures 5.5, 9.1–9.3

1857a *Hybocrinus tumidus* Billings, p. 275.
1858 *Hybocrinus pristinus* Billings, 1858, p. 25, figs. 4, 5.
1859 *Hybocrinus pristinus*; Billings, p. 23, pl. 1, fig. 2a.
1859 *Hybocrinus tumidus*; Billings, p. 28, pl. 2, fig. 1a–e.
1867 *Hybocrinus pristinus*; Grewingk, p. 103.
1867 *Hybocrinus tumidus*; Grewingk, p. 103.
1868 *Hybocrinus pristinus*; Shumard, p. 378.
1868 *Hybocrinus tumidus*; Shumard, p. 378.
1868 *Hybocrinus pristinus*; Bigsby, p. 20.
1868 *Hybocrinus tumidus*; Bigsby, p. 20.
1880 *Hybocrinus tumidus*; Wetherby, p. 152, pl. 5, fig. 2a–c.
1882 *Hybocrinus tumidus*; Carpenter, p. 298, fig. A, pl. 11, figs. 3–5.
1889 *Hybocrinus pristinus*; Miller, p. 255.
1889 *Hybocrinus tumidus*; Miller, p. 255.
1910 *Hybocrinus pristinus*; Grabau and Shimer, p. 501.
1910 *Hybocrinus tumidus*; Grabau and Shimer, p. 501, fig. 1812.
1915 *Hybocrinus pristinus*; Bassler, p. 654.
1915 *Hybocrinus tumidus*; Bassler, p. 654.
1943 *Hybocrinus pristinus*; Bassler and Moodey, p. 515.
1943 *Hybocrinus tumidus*; Bassler and Moodey, p. 515.
1944 *Hybocrinus tumidus*; Moore and Laudon, p. 151, pl. 53, fig. 3.
1946 *Hybocrinus tumidus*; Wilson, p. 31.
1973 *Hybocrinus tumidus*; Webster, p. 151.
1975 *Hybocrinus tumidus*; Strimple, p. 51, fig. 1.
1981 *Hybocrinus tumidus*; Parsley, p. 3, pl. 1, figs. 6, 9.
1986 *Hybocrinus tumidus*; Webster, p. 174.
1988 *Hybocrinus tumidus*; Webster, p. 96.
2013 *Hybocrinus tumidus*; Webster and Webster, p. 1666.
2013 *Hybocrinus pristinus*; Webster and Webster, p. 1665.

Type specimens.—Wilson (1946) recognized cotypes (GSC 1419b and 1419c) from Ottawa, Canada in the Trenton Limestone.

Diagnosis.—Calyx asymmetrical about oral-aboral axis; calyx with subpentagonal outline in oral view; calyx plate sculpture coarsely granulose; summit surface tilted; basal plates unequal in size; anal X nearly equidimensional or wider than high; distal margin of first anal plate with deep grooves; A-ray arm stout; position of column facet asymmetrical.

Occurrence.—*Hybocrinus tumidus* was originally described from the Cobourg beds (now Lindsay Formation) at Ottawa, Canada, and *H. pristinus* was originally described from the Aylmer Formation (Sandbian) of Quebec, Canada. In addition, this taxon was reported from the Hull (now Bobcaygeon Formation) and Sherman Falls members, Ottawa (now Verulam) Formation, Ontario (Katian), Canada; and the Curdsville Member, Hermitage Formation, Kentucky (Katian), USA. Since then, it has been recognized from the Curdsville Limestone Member of the Lexington Limestone in Mercer County, Kentucky, USA. In the Brechin Lagerstätte *H. tumidus* is known from the Bobcaygeon-Verulam contact zone at the Carden Quarry (UMMP 74669) and LaFarge Quarry and from the upper Bobcaygeon at the Kirkfield Quarry (Ordovician, Katian).

Description.—Crown medium-sized. Aboral cup medium bowl- to medium globe-shaped; maximum width to maximum height ratio ~1.0; plates gently to markedly convex; sculpture with irregular-shaped, small nodes arranged in rows parallel to plate boundaries, combined with fine pitting (Fig. 9.3); in narrow margin along plate boundaries, fine ridges perpendicular to plate boundaries that abut similar ridges on opposing plates.

Basal circlet ~25% of aboral cup height, varying in different rays. Basal plates five, hexagonal, very differently sized (Fig. 9.3), typically as high as wide. Radial circlet ~75% of aboral cup height; radial plates five, A, B, D, and E radial plates simple; C radial plate compound. Radial plates of very different sizes and shapes, symmetrical or asymmetrical about the oral-aboral axis. C inferradial hexagonal, slightly wider than high; superradial above to right; first anal plate above to left. Radial facets angustary, horseshoe-shaped, declivate; A, B, and E radial facets symmetrically positioned on radial plate; C and D radial facets asymmetrically positioned on radial plate. Details of radial facet topography unknown.

Radianal (Fig. 9.2) supported equally beneath by C and D inferradials, supporting above C radial plate to right and anal X to left. Anal X partially in aboral cup; distal margin arcuate, strongly crenulate (Figs. 5.5, 9.2). Oral surface plating unknown; surface tilted relative to oral-aboral axis.

Arms atomous; primibrachials rectilinear uniserial (Fig. 9.1), as high as wide, distinctly convex, deep; lateral sides of brachials strongly crenulate (Fig. 9.2).

Proximal columnals very thin, homeomorphic; wavy sutures between columnals; other aspects of column not known. Lumen strongly pentalobate, ~50% of columnal width; columnal facets unknown.

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Materials.—CMC IP 22560, 36433, and 55395; UMMP 74669, 74687.1, and 74687.2.

Measurements.—UMMP 74669: CrH, 30.5*; maximum ACH, 18.2; maximum ACW, 17.3; ArH, 16.2*; CoH, 3.1*.

Remarks.—In describing his new species *Hybocrinus pristinus*, Billings (1858, p. 24) noted: "This species so closely resembles *H. tumidus* of the Trenton Limestone, that I have had much doubt as to the propriety of separating it therefrom. The only differences that I can perceive are, that it is always smaller that the Trenton form, the plates more coarsely granulated under a lens, and not so convex in their centres [sic]. In a well-preserved specimen of *H. tumidus* the column exhibits from eight to ten joints in the length of one line, where as in *H. pristinus* there are only five. Under these circumstances I have thought it best to distinguish that Chazy specimens by a separate name for the present." This distinction recognized by Billings is readily explained by ontogenetic variation, and we consider *H. pristinus* to be a junior synonym of *H. tumidus*. Therefore, the Katian crinoid faunas have only two species of *Hybocrinus*, *H. conicus* and *H. tumidus*. These two Katian species are distinguished because *H. tumidus* has a summit surface that is tilted, basal plates unequal in size, the distal margin of the first anal plate with deep grooves, and an asymmetrical position of the column facet. In contrast, *H. conicus* has a summit surface that is not tilted, basal plates approximately equal in size, the distal margin of the first anal plate lacking deep grooves, and a symmetrical position of the column facet.

Family Hybocystitidae Jaekel, 1918

Genus *Hybocystites* Wetherby, 1880

Type species.—*Hybocystites problematicus* Wetherby, 1880, by monotypy.

Occurrence.—Ordovician (Katian), New York, USA and Ontario, Canada.

Remarks.—As noted below, *Hybocystites* is now considered monospecific with the recommendation herein that *H. problematicus* and *H. eldonensis* are conspecific.

Hybocystites problematicus Wetherby, 1880
Figure 9.6

1880 *Hybocystites problematicus* Wetherby, p. 7, pl. 5, fig. 1a–c.
1882 *Hybocystites problematicus*; Carpenter, p. 307, pl. 11, figs. 6–24.
1889 *Hybocystites problematicus*; Miller, p. 256, fig. 342.
1900 *Hybocystis problematicus*; Bather in Lankester, p. 95, fig. 1.
1908 *Hybocystites problematicus*; Parks, p. 232, pl. 2, figs. 1–3, 5.
1908 *Hybocystis eldonensis* Parks, p. 234, pl. 2, fig. 4.
1911 *Hybocystis eldonensis*; Springer, p. 13, pl. 2, figs. 1–10.
1915 *Hybocystites eldonensis*; Bassler, p. 654.
1915 *Hybocystites problematicus*; Bassler, p. 655.
1938 *Hybocystites problematicus*; Bassler, p. 115.
1943 *Hybocystites eldonensis*; Bassler and Moodey, p. 515.
1943 *Hybocystis problematicus*; Bassler and Moodey, p. 516.
1943 *Hybocystis eldonensis*; Bassler and Moodey, p. 515.
1943 *Hybocystites eldonensis*; Moore and Laudon, p. 130, pl. 1, fig. 8.
1944 *Hybocystites eldonensis*; Moore and Laudon, p. 151, pl. 53, fig. 1.
1948 *Hybocystis eldonensis*; Cuénot, p. 55, fig. 69.
1948 *Hybocystites problematicus*; Regnell, p. 9, fig. 3B.
1953 *Hybocystites eldonensis*; Ubaghs, p. 749, figs. 143, 144.
1953 *Hybocystites problematicus*; Ubaghs, p. 749, fig. 80c.
1973 *Hybocystites eldonensis*; Webster, p. 152.
1973 *Hybocystites problematicus*; Webster, p. 152.
1975 *Hybocystites problematicus*; Strimple, p. 51, fig. 1.
1978 *Hybocystites eldonensis*; Brett and Liddell, p. 338, figs. 5.8, 7–9.
1978 *Hybocystites problematicus*; Sprinkle and Moore, p. T572, fig. 365.1a, b.
1978 *Hybocystites eldonensis*; Ubaghs, p. T138, figs. 109.5–109.6, 151.4, 174.11.
1978 *Hybocystites eldonensis*; Sprinkle and Moore, p. T574, fig. 365.1c–j.
1981 *Hybocystites problematicus*; Parsley, p. 4, pl. 1, figs. 7, 8, 10.
1981 *Hybocystites problematicus*; Arendt, p. 164, fig. 29b.
1981 *Hybocystites eldonensis*; Arendt, p. 164, fig. 29e–zh.
1985 *Hybocystites eldonensis*; Rozhnov, p. 5, fig. 1d.
1985 *Hybocystis eldonensis*; Smith, p. 170, pl. 7.4.22.
1986 *Hybocystites eldonensis*; Rozhnov, p. 1, fig. 1e.
1986 *Hybocystites problematicus*; Webster, p. 174.
1986 *Hybocystites eldonensis*; Webster, p. 174.
1988 *Hybocystites problematicus*; Webster, p. 96.
1988 *Hybocystites eldonensis*; Webster, p. 96.
1993 *Hybocystites eldonensis*; Webster, p. 70.
1999 *Hybocystites eldonensis*; Brett and Taylor, p. 69, fig. 79.
2002 *Hybocystites eldonensis*; Rozhnov, p. 584, fig. 44e.

Holotype.—The holotype of *Hybocystites problematicus* has not been located with certainty; the holotype of *H. eldonensis* is ROM 23779.

Occurrence.—Wetherby's original specimens of *Hybocystites problematicus* were reportedly from the upper Trenton (Katian) in Mercer County, Kentucky, USA, and *H. eldonensis* was originally reported from Kirkfield, Ontario, Canada. This taxon is now known from the Curdsville Member of the Hermitage Formation (Katian) in Anderson, Garrard, Hermitage, and Jessamine counties in Kentucky; the Hull Member of the Ottawa (now Bobcaygeon) Formation and the Bobcaygeon Formation at Kirkfield, Ontario. New material is from the Bobcaygeon-Verulam contact zone at the Carden Quarry (UMMP 74670) (Ordovician, Katian).

Description.—Crown medium-sized. Aboral cup medium globe-shaped (Fig. 9.6); maximum width to maximum height ratio ~1.0; all plates with coarse sculpture as noted below.

Basal circlet ~33% of aboral cup height. Basal plates five, pentagonal, equal in size, as high as wide; coarsely nodose plate sculpture that can be irregular or roughly arranged in rows

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parallel to plate boundaries. Radial circlet ~67% of aboral cup height; radial plates five, A, B, D, and E radial plates simple, of approximately same size and shape; symmetrical about oral-aboral axis; C radial plate compound. A, C, and D radial plates supporting a free arm; B and E radial plates lacking a free arm, but each with recumbent ambulacrum. Sculpture of A, C, and D radial plates only coarse irregular nodes of similar size across plates (Fig. 9.6). Sculpture of B and E radial plates with coarse nodes marginally; large nodes toward plate center merging into coarse ridges that abut and are arranged perpendicular to recumbent ambulacra. C inferradial hexagonal, approximately as high as wide; superradial above to right; first anal plate above to left. Radial facets angustary, horseshoe-shaped, declivate; details of radial facet topography unknown.

Posterior interray and tegmen plating unknown on present material; surface presumably perpendicular to oral-aboral axis.

Atomous free arms three (A, C, and D rays). Primibrachials rectilinear uniserial, as high as wide, >3.0 times deeper than wide proximally, as deep as wide distally; lateral sides of brachials with coarse irregular nodes and ridges that define a groove admedially along side of each brachial (Fig. 9.6). On rays with free arms (A, C, and D), ambulacra extending distally along adoral side of arm, over distal tip of arm, proximally along aboral side of arm, onto radial plate surface, and typically onto surface of basal plate. In some instances, ambulacrum extending onto proximal surface. On rays without free arms, ambulacra typically extending proximally onto basal plates and can extend onto column (Fig. 9.6). Biserial cover plates covering ambulacra.

Proximal columnals very thin, heteromorphic, holomeric, convex latus; proximal columnals very low, becoming higher distally. Lumen morphology and columnal facet morphology unknown.

Materials.—As noted above, the original Wetherby (1880) specimens have not been located, but existing collections include those from Springer (1911): USNM S 2051 and 2051; from Sprinkle (1973): USNM S 5732–5734; and from Parsley (1981): USNM 245187 and 245189. New specimens include UMMP 74670.1–74670.5 and 74687.3.

Measurements.—UMMP 74670.1: CrH, 28.0*; CaW, 18.5*; CoH, 10.0*. UMMP 74670.2: CrH, 25.3; CaH, 13.2; CaW, 17.0*; CoH, 8.0*. UMMP 74670.3: CaW, 18.6; CoH, 10.0*. Brechin UMMP 74670.4: CrH, 27.6*; CaH, 16.2; CaW, 20.1*; CoH, 13.0*. UMMP 74670.5: CrH, 28.6;* CaH, 21.0; CaW, 20.7; CoH, 12.5*.

Remarks.—Two species of *Hybocystites* are recognized, *H. problematicus* (originally described from Kentucky, USA) and *H. eldonensis* (originally described from Ontario, Canada). The type specimen of *H. eldonensis* was "only about seven millimeters in vertical extent" (Parks, 1908, p. 234), and it was differentiated from the type species by having the two recumbent ambulacra confined to the radial plates, and an ambulacral furrow that does not extend proximally to radial plates in arm-bearing rays. The Parks species also has much more subdued aboral plate sculpture than *H. problematicus*. Springer (1911) made a convincing argument that the differences between *H. problematicus* and *H. eldonensis* can be explained as ontogenetic changes. Further, in both Kentucky and Kirkfield, Ontario, single clusters of *Hybocystites* specimens contained both *H. problematicus* and *H. eldonensis* forms. Springer suggested that these two taxa are conspecific. He stated, "In view of the fact that Dr. Parks was the first to investigate and describe the Canadian forms, I prefer to place the foregoing facts at his disposal and leave the decision of the question to him, hoping that he will publish his conclusion; but the weight of evidence seems to me to favour the latter view" (Springer, 1911, p. 21, 22). Parks did not address this question in subsequent publications. Also, note that both the *H. problematicus* and *H. eldonensis* forms co-exist in the Brechin material.

Parsley (1981) followed Springer's conclusions and designated *Hybocystites eldonensis* as a junior synonym of *H. problematicus.* Synonymy of these two species has not always been followed (e.g., Webster and Webster, 2013), but we agree with Springer (1911) and Parsley (1981) that the 'weight of evidence' supports the position that these two species are conspecific.

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Accessibility of supplemental data

Data available from the Dryad Digital Repository: https://doi:10.5061/dryad.dm67f.

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