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The Revised Systematics and Paleoecology of the Devonian Stemless Crinoid Genus *Edriocrinus* Hall, 1858

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THE REVISED SYSTEMATICS AND PALEOECOLOGY OF THE DEVONIAN STEMLESS CRINOID GENUS *EDRIOCRINUS* HALL, 1858

THESIS

A thesis submitted in partial fulfillment of the
requirements for the degree of Master of Science in the
College of Arts and Sciences
at the University of Kentucky

By

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2022

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ABSTRACT OF THESIS

THE REVISED SYSTEMATICS AND PALEOECOLOGY OF THE DEVONIAN STEMLESS CRINOID GENUS *EDRIOCRINUS* HALL, 1858

New morphological observations of *Edriocrinus* Hall, 1858, enable a modern, holistic view of this unusual crinoid genus, previously included in the Superorder Flexibilia (Zittel, 1895) Wright et al., 2017. Re-analysis of *Edriocrinus* suggests that the genus should now be assigned to the Order 'Dendrocrinida' within the Magnorder Eucladida Wright, 2017 based on the five infrabasals, single radianal in the cup, absent anal sac, and non-pinnulate arms with rectangular uniserial brachials. Moreover, examination of the slight variations separating the current 14 *Edriocrinus* species indicates that these "species" are likely ecophenotypes. The current *Edriocrinus* species are revised based on firmly bound calyx plates; five high infrabasals; lack of patelloid processes; straight muscular radial articulations; brachials that are free above the radials; and muscular articulation between brachials and synonymized to four species, *E. pocilliformis, E. sacculus, E. pyriformis,* and *E. dispansus.*

Edriocrinus is restricted to a ~25 Myr interval in the Early and Middle Devonian, a time of global eustatic and tectonic disruption, when its stemlessness provided an adaptive advantage throughout environments in the Old World and Eastern Americas realms. These realms were in subtropical to warm temperate climatic zones that encompassed the Rheic Ocean between 25°and 35° south latitude. *Edriocrinus* is found in formerly adjacent parts of east-central North America, south-central Europe, southern England, and northern Africa. The genus persisted in south-central Europe until the Chotec Event in early Eifelian time and in North America until the Bakoven Event in mid-Eifelian time, when episodes of transgression and anoxia led to genus extinction.

KEYWORDS: Paleozoic, Lower and Middle Devonian, stemless crinoids, systematics, paleobiogeographic realms, biotic interactions

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CHAPTER 1. INTRODUCTION

Widespread agreement exists that *Edriocrinus* Hall, 1858, is quite unusual among crinoids (Hall, 1859; e.g., Meek and Worthen, 1868; Kayser, 1885; Wachsmuth and Springer, 1886; Nicholson and Lydekker, 1889; Jaekel, 1899, 1914; Schlüter, 1900; Talbot, 1905; Kirk, 1911; Wanner, 1915; Dunbar, 1919; Springer, 1920; Ehrenberg, 1928; Goldring, 1938; Moore and Laudon, 1943; Shimer and Shrock, 1944; Gross, 1948; Le Maître, 1958a, b; Van Sant and Lane, 1964; Witzke et al., 1979; McIntosh, 1981; Frest et al., 1999; Seilacher and MacClintock, 2005; Prokop and Turek, 2014; Clement and Brett, 2015). This enigmatic stemless crinoid genus is currently classified in the crinoid Superorder Flexibilia (Zittel, 1895) Wright et al., 2017, order uncertain (Strimple in Moore and Teichert, 1978). Some specimens are so unusual that they were originally classified as sponges (Kayser, 1885; Jaekel, 1899, 1914; Wanner, 1915) or as cystoids (Jaekel, 1899; Kesling in Moore, 1967). Even classified as a crinoid, *Edriocrinus* is enigmatic because it is a stemless Paleozoic crinoid, and its taxonomic status remains uncertain. Its current designation as a flexible crinoid is ambiguous at best. The strange genus has been known since 1858 (Hall in Silliman et al., 1858) from Lower and Middle Devonian rocks of central and eastern North America (Hall in Silliman et al., 1858; Hall, 1859, 1862; Wachsmuth and Springer, 1886; Carpenter, 1887; Nicholson, 1889; Bather, 1900; Clarke, 1900; Weller, 1900; Foerste, 1903; Kirk, 1911; Dunbar, 1919; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Cleaves, 1939; Strimple, 1963; Prokop, 1976; Strimple, 1977; Strimple in Moore and Teichert, 1978; Witzke et al., 1979; McIntosh, 1981; Ettensohn, 1984;

Prokop and Petr, 1995a, b; Seilacher and MacClintock, 2005; Parsley and Sumrall, 2007; Prokop and Turek, 2014; Clement and Brett, 2015); northern Africa (LeMaître, 1958; Prokop, 1976; Strimple, 1977; Strimple in Moore and Teichert, 1978; Ettensohn, 1984; Prokop and Turek, 2014); and south-central Europe and southern England (Kayser, 1885; Jaekel, 1899, 1914; Bather, 1900, 1928; Green and Sherborn, 1906; Wanner, 1915; Springer, 1920; Ehrenberg, 1928; Strimple, 1963; Prokop, 1976; Strimple, 1977; Strimple in Moore and Teichert, 1978; McIntosh, 1981; Ettensohn, 1984; Prokop, 1987; Prokop and Petr 1995a, b; Prokop and Turek, 2014) (Fig. 1.1).

The first described fossil specimens and the type species, *Edriocrinus pocilliformis,* came from Devonian shaly limestones of the New Scotland Formation in the Helderberg Group in New York (Hall, 1859; Springer, 1920). Worldwide, the genus is restricted to Lower and Middle Devonian clastic and carbonate rocks. *Edriocrinus,* as currently designated, lived in subtropical seas of eastern and central Laurussia (now eastern and central USA, southern England, and parts of central Europe), lived near northwestern Gondwana (Bohemia, now central Europe), and lived in the warm temperate seas of northwestern Gondwana (now northern Africa). Ancient oceanic currents may have connected the shallow seas near the two continents (Fig. 1.1), enabling larval dispersal (e.g., Witzke et al., 1979).

The unusual features of *Edriocrinus*, as currently designated, include: (1) a stemless nature in adulthood; (2) incurved, anomalously wide arms where known; and (3) a cup made of fused, laminated plates with an unusually thick layer of calcite secreted during life at the distal (aboral) end of the cup (Hall in Silliman et al., 1858, Hall, 1859, 1862; Jaekel, 1914; Springer, 1920; Goldring, 1923; Ehrenberg, 1928). In particular, *Edriocrinus* is best known for its stemless nature. Stemlessness may include mobile, free-living adult forms or those which remained attached directly to the substrate by the cup throughout their lives (Hall in Silliman et al., 1858; Hall, 1859, 1862; Schlüter, 1878; Wachsmuth and Springer, 1886; Carpenter, 1887; Nicholson, 1889; Bather, 1900; Kirk, 1911; Jaekel, 1914; Wanner, 1915; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Strimple, 1963; Prokop, 1976; Strimple, 1977; Strimple in Moore and Teichert, 1978; Ettensohn, 1984; Prokop and Petr, 1995a; Seilacher and Hauff, 2004; Seilacher and MacClintock, 2005; Prokop and Turek, 2014; Clement and Brett, 2015). Similarly stemless, but mobile, crinoids predominate in Cenozoic and modern seas (Moore et al., 1952; Shrock and Twenhofel, 1953; Janevski and Baumiller, 2010; e.g., Baumiller et al., 2010; Gorzelak et al., 2012), but stemlessness was abnormal among most crinoids during Paleozoic and early Mesozoic time (Shrock and Twenhofel, 1953; Ettensohn, 1975, 1981, 1984; e.g., Baumiller et al., 2010; Gorzelak et al., 2012). Also, all *Edriocrinus* species seem to have added calcite to the cup as internal or external laminae, whereas most crinoids typically add calcite at all plate margins during their growth (Fig. 1.3C, D, E). Some previous workers described specimens with such laminae as “concentrically striated” (Hall, 1859, p. 121; Prokop, 1976, p. 189).

1.1 An ambiguous classification: What is *Edriocrinus*?

The genus *Edriocrinus* is currently assigned to the Superorder Flexibilia (discussed in Chapter 4) almost exclusively based on the shape and width of its uniserial, nonpinnulate arms (Moore and Laudon, 1943) (Fig. 1.2A, B, C). However, only two *Edriocrinus* species, the free-living *E. sacculus* and attached *E. holopoides,* have preserved arms (Springer, 1920). In fact, the type species, *E. pocilliformis,* as subsequently designated by Miller (1889), bears no preserved arms. Typically, a distinguishing characteristic of flexible crinoids is the patelloid process (a tongue-and-groove structure; Fig. 1.2D), which separates the brachial plates of flexible arms but is unknown in the genus *Edriocrinus.* In addition, crinoids in the Superorder Flexibilia display the widest arms of all crinoid taxa, but the arms of *Edriocrinus* are unusually wide, even compared with other flexible crinoids (Springer, 1920; Moore in Moore and Teichert, 1978; Strimple in Moore and Teichert, 1978) (Fig. 1.3A, B, Fig. 4.1J, L). Hence, the current placement of *Edriocrinus* within the Flexibilia may be unfounded based on a few preserved arms (e.g., Bather, 1900; Kirk, 1911; Jaekel, 1914; Springer, 1920; Goldring, 1923; Moore and Laudon, 1943; Strimple in Moore and Teichert, 1978). Another notable characteristic among most flexible crinoids is the loosely bound calyx plates (Moore et al., 1952; Ausich and Meyer, 1992), as the name Flexibilia implies. *Edriocrinus*, in contrast, has tightly fused sutures between its calyx plates (Fig. 1.3A).

Edriocrinus does share some characteristics of the cup with other Paleozoic stemless crinoids. For example, the cups of some unrelated Paleozoic stemless genera were fused, distally thickened, or both (Bather, 1896, 1900; Kirk, 1911; Ubaughs in Moore and Teichert, 1978; Ettensohn, 1981, 1984; Seilacher and Hauff, 2004; Seilacher and MacClintock, 2005). Cup features have been used as a basis for generic description (e.g., Moore, Lane, and Strimple in Moore and Teichert, 1978). However, such features of the cup could reflect convergent evolution for similar environments; therefore, cup features would not necessarily be reliable taxobases for demonstrating relationships between *Edriocrinus* and other crinoids (Ettensohn, 1981). Further, cup morphology could be a dynamic, ecophenotypic trait, which would also be unsuitable as the foundation of a reliable, consistent classification (Ettensohn, 1980). Hence, some paleontologists have called for reconsideration of Paleozoic stemless crinoids, particularly *Edriocrinus*, as scientists have advanced toward phylogenetic systematics based on more consistent and better understood characters, such as those associated with the arms (Lane, 1989; e.g., Webster and Maples, 2008).

The majority of *Edriocrinus* species are known only from the basal parts of cups from the attached species and some free-living species (Fig. 1.4A–F, H, I). Most of the currently assigned species lack preserved arms, which are critical for classification. In addition to the taxonomic ambiguities, establishing agreement about the environmental and life-mode preferences of a genus like *Edriocrinus* has been especially challenging.

1.2 An ambiguous lifestyle

Workers have suggested several possible lifestyles for *Edriocrinus*. Some researchers have suggested that *Edriocrinus* cups may have included juvenile and adult specimens firmly attached or cemented to a substrate (Hall in Silliman et al., 1858, Hall, 1859, 1862; Schlüter, 1878; Wachsmuth and Springer, 1886; Carpenter, 1887; Nicholson, 1889; Bather, 1900; Kirk, 1911; e.g., Jaekel, 1914; Wanner, 1915; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Strimple, 1963; Prokop, 1976; Strimple, 1977; Strimple in Moore and Teichert, 1978; Prokop and Petr, 1995a; Seilacher and Hauff, 2004; Seilacher and MacClintock, 2005; Prokop and Turek, 2014; Clement and Brett, 2015) (Fig. 1.4A, H, I); others have suggested the ballasted cups of adult *Edriocrinus* (Bather, 1896) may have been inserted into or rested upon substrates where conditions were favorable (Strimple in

Moore and Teichert, 1978; Ettensohn, 1984; Seilacher and Hauff, 2004; Seilacher and MacClintock, 2005; Prokop and Turek, 2014). Certainly, paleontologists have reported cemented or infaunal modes of life among other Paleozoic stemless crinoid genera (Ettensohn, 1975, 1980, 1981, 1984; Brower, 1987; Seilacher and MacClintock, 2005). Furthermore, researchers have inferred relationships between morphology and the environment in which Paleozoic stemless crinoids lived (e.g., Bather, 1900; Jaekel, 1914; Ettensohn, 1975; Breimer in Moore and Teichert, 1978; Ettensohn, 1980; 1981; 1984). Parts of the cup may be useful as an indicator of lifestyle; much of the previous work on the lifestyle and classification of *Edriocrinus* has focused on the preserved, lower (aboral) parts of the cup, favored by taphonomic bias (e.g., Deline and Thomka, 2017).

Additionally, if *Edriocrinus* were mobile, it would certainly not be unique among crinoids of the past or present. Some workers have interpreted other fossil stemless crinoids as mobile (Bather, 1900; Ettensohn, 1984), and mobility is even documented among modern stemmed crinoids (Janevski and Baumiller, 2010). Mobility is one potential adaptation allowing crinoids to meet various environmental and ecological needs (Ettensohn, 1975; Baumiller et al., 2010; Gorzelak et al., 2012). Therefore, the possible mobility of some *Edriocrinus* species could hint at their environmental and ecological preferences. Indeed, relationships may exist between the nature of the arms or cup and the preferred substrate or geographic distribution.

For example, the robust arms of *E. sacculus* may merely have been an evolutionary response to the high-energy environment (Ettensohn, 1984). Other species occur in different lithologies, such as limestones (calcarenites–calcilutites) and shales, which probably represent different environments (e.g., Hall, 1859; Clarke, 1900; Foerste, 1903; Kirk, 1911; Dunbar, 1919, 1920; Goldring, 1923; Ehrenberg, 1928; Strimple, 1963; Prokop, 1976; Ettensohn, 1984; Prokop, 1987; Prokop and Petr, 1995a, b; Prokop and Turek, 2014; Clement and Brett, 2015). If different species lived in different environments, they may not have all lived in the same manner. Further study of the different paleoenvironments in which specimens have been found could also help answer the question of the ecological range of *Edriocrinus,* which is not yet clearly understood.

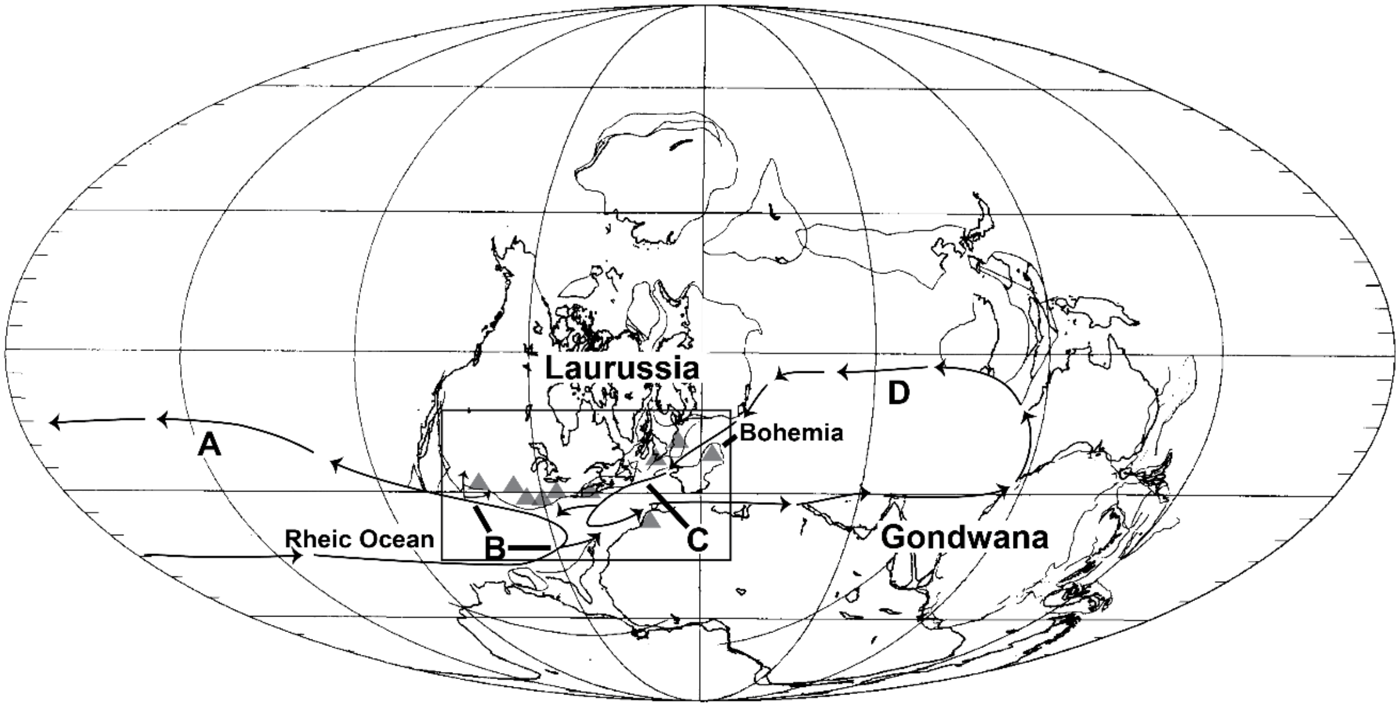

Figure 1.1 Distribution of *Edriocrinus*, marked with triangles, and paleocurrents of Early–Middle Devonian time.
A: Cool subtropical gyre. B: South west-wind drift. C: Western boundary current. D: Warm subtropical gyre. (Modified from Scotese and McKerrow, 1990; currents after Heckel and Witzke, 1979).

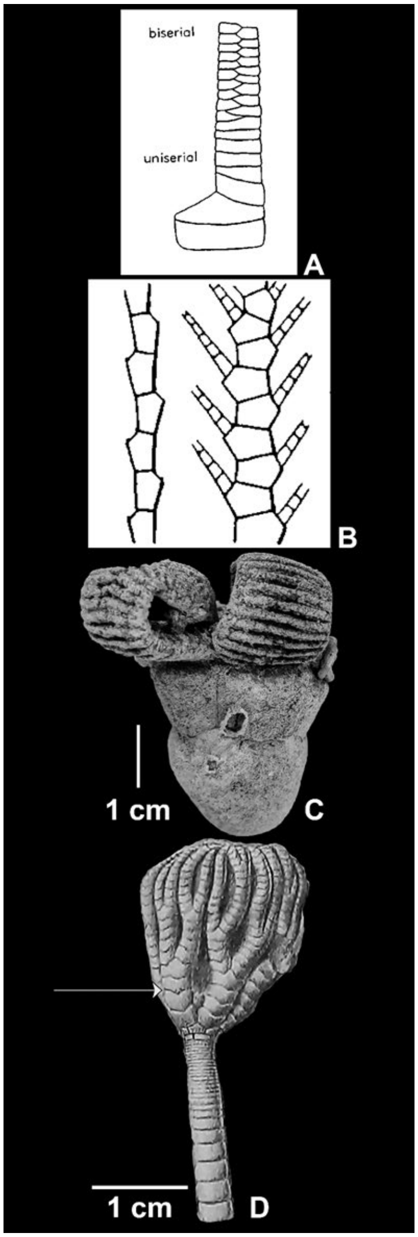

Figure 1.2 Arm characters of crinoids, *Edriocrinus*, and flexibles.

A: Uniserial and biserial arrangement of brachials. B: Nonpinnulate (left) and pinnulate (right) arms. C: Uniserial, nonpinnulate arms of *E. sacculus*, USNM 178672. D: Arrow indicating patelloid process between brachials of *Taxocrinus communis*. (A and B modified from Ubaghs in Moore and Teichert, 1978; D modified from Springer, 1920).

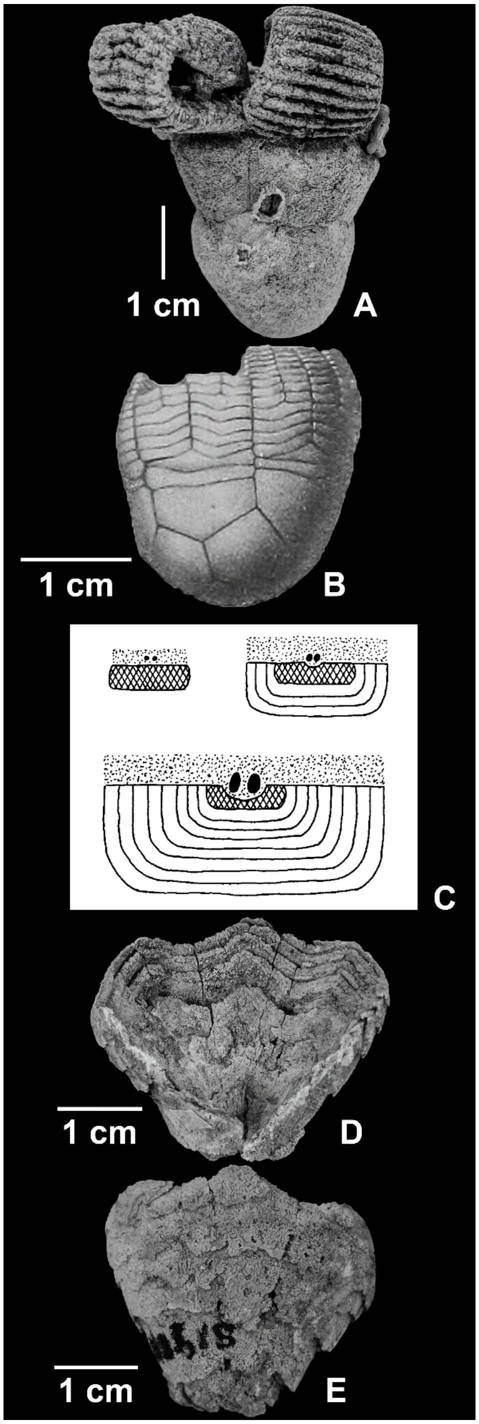

Figure 1.3. Arm width of *Edriocrinus* and flexibles and plate growth of crinoids and *Edriocrinus*. A: Wide arms of E. sacculus, USNM 178672. B: Wide arms and primibrachials of *Lecanocrinus macropetalus*. C: Typical crinoid plate growth, youngest to oldest clockwise from top left. Soft parts on plate interiors stippled, axial nerve cords black, embryonic plates cross-ruled (Brower in Moore and Teichert, 1978). D: Internal laminae of *E. sacculus*, USNM 1910. E: External laminae of USNM 1910. (B modified from Springer, 1920; C modified from Brower in Moore and Teichert, 1978).

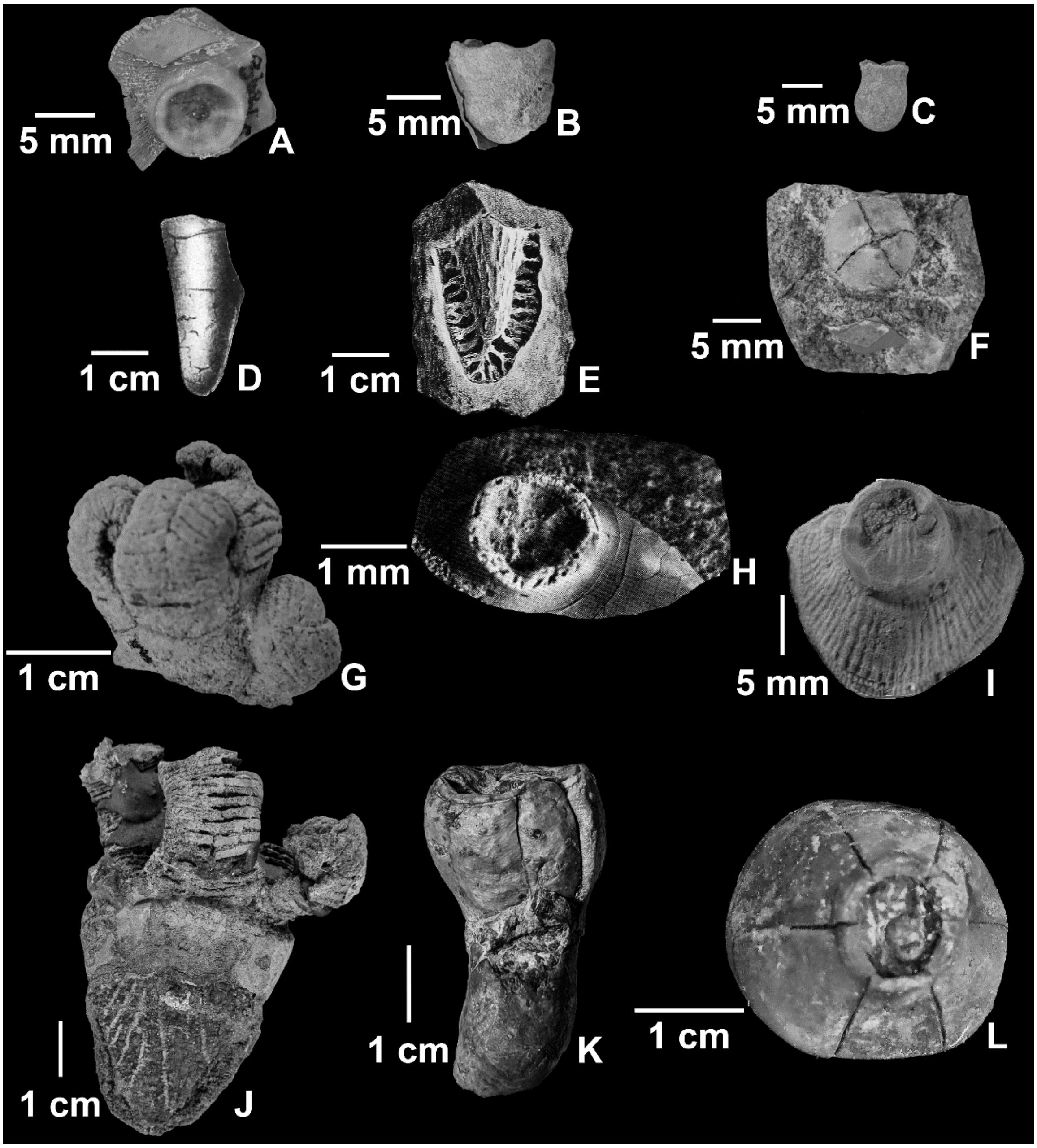

Figure 1.4. Currently recognized species of the genus *Edriocrinus*. A: *E. adhaerens* Springer, 1920. Syntype, USNM 1898. B: *E. pocilliformis* Hall, 1859 USNM 97727. C: *E. occidentalis* Springer, 1920. Syntype, USNM 1902. D: *E. becraftensis* Clarke, 1900. E: *Lodanella mira* Kayser, 1885. F: *E. explicatus* Springer, 1920. Syntype, USNM 1900. G: *E. holopoides* Springer, 1920. Syntype, USNM 1901. H: *E. ata,* syn. *E. cylindricus* and *E. tara,* Prokop, 1976. I: *E. adnascens* Dunbar, 1920. J: *E. sacculus* Hall, 1859*,* USNM 1910. K: *E. pyriformis* Hall, 1862. Onomatype, CMCIP 37144. L: *E. dispansus* Kirk, 1911. Holotype, USNM 27757. (D modified from Ehrenberg, 1928; E modified from Kayser, 1885; H modified from Prokop, 1976; I modified from Clement and Brett, 2015).

CHAPTER 2. THE PROBLEM WITH *EDRIOCRINUS* HALL, 1858

Previous workers have only been able to agree that *Edriocrinus* is a crinoid. Because most aspects of its classification and lifestyle are uncertain, the subject of this study is to establish some certainty about these bizarre crinoids.

2.1 Hypothesis

The genus *Edriocrinus* warrants a thorough re-examination (Prokop, 1976). Some paleontologists have seemingly assigned species to this genus and attempted to establish relationships with other crinoids based exclusively on their stemlessness (Wachsmuth and Springer, 1886; Carpenter, 1887; Talbot, 1905; Springer, 1920) with little to no knowledge of their arms and calyces. Stemlessness alone is certainly an inadequate taxobasis, and it may even reflect a homoplasic character with no taxonomic value. Furthermore, if species (Fig. 1.4) are to be associated with *Edriocrinus,* then preserved arm attachments and any preserved arms need to be considered, because they may yield additional valuable information. For example, one species, *Edriocrinus sacculus,* was interpreted to walk upside-down partly because its uniquely wide arms have been preserved (Kirk, 1911, Kesling and Mintz, 1961). The development of its arms, however, may only reflect the nature of the environments in which the crinoids lived, the available diet, and the compatible feeding strategies (Ettensohn, 1975).

The central question of this study is simply, what is *Edriocrinus* and how did it live? This unusual crinoid genus does not resemble typical flexible crinoids (Fig. 1.2C, D). Stemlessness and arm shape are not always suitable taxobases and such characters may have been misapplied in designating the genus *Edriocrinus* and its species. The related hypotheses are that *Edriocrinus* is not a flexible crinoid, and that its unusual morphology is a product of environmental factors. Additionally, if the generic and specific designations of this crinoid can be revised with more pertinent taxobases, its status as a stemless crinoid which is not a flexible can be clarified and its habitats better understood.

2.2 Methods

To that end, I reviewed literature on the systematics of *Edriocrinus* to determine how flexible crinoids and different *Edriocrinus* species were defined. I examined, measured, and photographed holotypes, other type specimens of each species, and many other available specimens in museums where possible. I compared these specimens with each other and to published descriptions, including those of typical flexible crinoids. Where it was not possible to examine a type specimen, I studied the defining literature for taxobases that are perhaps better suited for the definition of *Edriocrinus* species. With these taxobases, I revised and updated each species description. More robust taxobases are needed to reinforce the application of modern cladistic methods to this genus.

Repositories and institutional abbreviations. —Types, figured, and other specimens examined herein are deposited in the following institutions: Cincinnati Museum Center (CMCIP), Cincinnati, USA; National Museum of Natural History (USNM), Washington, D.C., USA; American Museum of Natural History (AMNH), New York, USA; The Field Museum (The Field Museum), Chicago, USA; University of Illinois (C, SUI).

CHAPTER 3. ORIGINAL SYSTEMATIC PALEONTOLOGY OF *EDRIOCRINUS*

Edriocrinus has been classified as a genus in the Subclass Flexibilia (Moore in Moore and Teichert, 1978, Strimple in Moore and Teichert, 1978). The taxonomic history is summarized as follows to better understand the different criteria which have been used as taxobases for classification.

3.1 Previous classification

Phylum Echinodermata

Class Crinoidea Miller, 1821

Subclass Flexibilia? Zittel, 1895

Order Uncertain

Family Edriocrinidae Miller, 1889 (*non* Edriocrinidae Talbot, 1905)

Genus *Edriocrinus* Hall, 1858

Type species. — *Edriocrinus pocilliformis* Hall, 1859, by subsequent designation and position precedence

Hall (1859) designated the genus *Edriocrinus* with two species, *E. pocilliformis* and *E. sacculus*, but provided no further taxonomic assignment for *Edriocrinus*. The original description included terms and usage that are vague and outdated by modern standards. In the description, the word "pinnules" almost certainly meant "arms." Hall (1852) gave a definition of "tentacula" that was the same as the definition of "pinnules" in modern usage. The "proboscis" was most likely the "anal tube" in modern terminology. Hall (in Silliman et al., 1858, p. 278) gave the following description based on the species *E. pocilliformis* and *E. sacculus.* The description of the arms was derived from *E. sacculus* because the arms of *E. pocilliformis* were not evident at this time.

> "Body subconical. Base solid, without division into plates: upper margin marked by six angles, with depressions between for insertion of radial plates. Radial plates five, inserted in the five larger depressions on the upper edge of the calyx. Anal plates two, the lower one inserted in the smaller of the six impressions on the upper margin of the calyx; the second anal plate placed on the upper edge of the first. Brachial plates numerous, consisting of thin plates in consecutive series resting upon the upper concave edges of the radial plates: pinnules subdivided above. Tentacula unknown. Proboscis unknown. Column none."

Hall never formally designated a type species for the genus, but *E. pocilliformis* was the first species to appear in Hall's (1859) description. Accordingly, by ICZN 69.1 (subsequent designation) and ICZN 69A.10 (position precedence), Miller (1889) designated *E. pocilliformis* as the type species (ICZN, 1999). Wachsmuth and Springer (1886) gave *E. sacculus* as the type species, but it did not have position precedence. Hall asserted that *Edriocrinus* did not have a stem at any point in its life. Therefore, he interpreted the attachment scar as evidence that the juveniles, either alone or together in small groups of two or three, were attached by the base and detached at maturity. In 1862, Hall described and added a new species to the genus, *E. pyriformis,* and maintained that it lacked a stem throughout its life. Based on Hall's (1859) original *E. sacculus* specimens, Wachsmuth and Springer (1879) reported that the arm structure of *Euspirocrinus,* now a eucladid, was similar to that of *Edriocrinus* and the modern stemless genus *Holopus* (Fig. 3.1C, D).

Shortly thereafter, similar European specimens were misidentified as sponges and placed in the genus *Lodanella* (Kayser, 1885). A higher classification was first attempted by Wachsmuth and Springer (1886), who classified *Edriocrinus* and other stemless crinoids in the Suborder Inadunata Wachsmuth and Springer, 1886. Within this suborder, they also erected subtaxa which they called “branches.” They classified *Edriocrinus* in the Branch Fistulata, which was characterized by the presence of ventral, perisomal plates with pores. However, this placement was not consistent with the preserved features of *Edriocrinus;* as Wachsmuth and Springer (1886, p. 189–190) noted in the following diagnosis, no ventral structure of the genus has ever been observed.

> “Generic diagnosis, etc.-Sessile in its larval state; free-floating in the adult, being attached by the lower end of the basals.
>
> Basals unusually large, elongate, closely anchylosed so as to show no suture lines at the outer face; internally, however, there are indications that the base might have been bisected. In the young animal the form of the base is irregular and linear, in the adult subglobose or deeply bowl-shaped, and the scar by which the animal was attached, becomes totally obliterated by heavy deposits of calcareous matter. Owing to this deposit the outer form of the base differs considerably from the form of the inner cavity, which grows gradually narrower toward the bottom, and frequently ends in a sharp point. The walls are massive at their lower parts, thin at the upper edge, which shows six excavated faces for the attachment of five radials and an anal plate.
>
> Radials comparatively small, quadrangular, articular facet but slightly excavated, occupying the full width of the plates; provided with a transverse articular ridge. The anal plate is in line with, and has the length of the radials, but is narrower; it supports a small plate, but beyond that nothing is known of the anal apparatus. The structure of the ventral surface has not been observed.
>
> The arms are broad at the base, composed of extremely short transverse pieces, of which ten or more occur between the first bifurcation. Nothing is known of pinnules, nor of the condition of the ventral furrow.”

Within the Suborder Inadunata, Branch Fistulata, they placed the stemless genus *Agassizocrinus* in the Family Astylocrinidae. They also “provisionally” placed *Edriocrinus* in the same family because both genera were stemless at maturity with distally fused and thickened cups. However, *Agassizocrinus* was known to be dicyclic (bearing two circlets of plates below the radials), whereas they considered *Edriocrinus* to be monocyclic (bearing one circlet of plates below the radials) and attached without a stem during its juvenile stages. Hence, they foresaw that *Edriocrinus* would prove to be so unique that it would need its own family designation. The Family Astylocrinidae was only the first of three proposed families for the genus *Edriocrinus.* Wachsmuth and Springer also noted two anal plates in the genus and a similarity between the cups of young *Edriocrinus* and the fused base of the modern, attached, stemless articulate genus *Holopus* d'Orbigny, 1837. *Holopus* appears to have an entirely fused cup (Carpenter, 1887; Nicholson and Lydekker, 1889; Bather, 1900; Donovan, 2006; Donovan and Pawson, 2008; Hess *in* Selden, 2011) (Fig. 3.1C).

Carpenter (1887) also discussed the resemblance between *Edriocrinus* and *Holopus;* he even suggested that *Edriocrinus* and *Holopus* were closely related, because both genera have stemless, attached cups. Thirty years after the genus was created, Miller (1889) created the family Edriocrinidae, of which *Edriocrinus* remains the sole member. This was the second family designation for the genus. Like Hall (in Silliman et al., 1858; Hall, 1859) and Wachsmuth and Springer (1886), he also noted that two anal plates were present in the genus. The Flexibilia were subsequently defined by Zittel in 1895, and researchers soon took advantage of this crinoid taxon. Although previous workers had noted the unusually thick stereom at the distal end of the cup, Bather (1896) was apparently the first to propose that the thick deposit functioned as ballast. Jaekel (1899) recognized that *Lodanella* was not a sponge and classified it as a cystoid because an apparent system of pores was preserved.

The first worker to associate *Edriocrinus* with the flexibles was Bather (1900), who placed *Edriocrinus* “provisionally” in the “Grade” Impinnata, which he considered to be a subdivision of the Flexibilia. Bather (1900) also suggested that young *Edriocrinus* were attached directly by the basal plates, which fused into a “bowl-shaped mass” at maturity. Regarding classification, nearly all workers since 1900 have remained similarly uncertain about *Edriocrinus.* Some have noted (e.g., Clement and Brett, 2015) that its arms are similar to those of flexibles, but many workers have assigned it an uncertain status within the flexibles.

Nevertheless, five years later, Talbot (1905) attempted the first major revision of the genus. Her generic description was more modern and thorough. She included an updated nomenclature and usage for morphologic features of the crinoid. The use of the term “pinnules” matches the modern usage of the term, and this description was based on the species *E. sacculus* and *E. pocilliformis.* Talbot reported two anal plates in the genus. Because she noted the presence of infrabasals, she also suggested that at least some *Edriocrinus* were dicyclic, with infrabasals that fused at maturity like those of *Agassizocrinus*. She agreed with Wachsmuth and Springer (1886) that *Edriocrinus* should remain in the Suborder Inadunata, “Branch Fistulata.” However, she disagreed with Wachsmuth and Springer’s (1886) placement of *Edriocrinus* in the Astylocrinidae. The absence of supplementary anal plates meant it could not be in the Family Astylocrinidae with *Agassizocrinus.* She also disagreed with Bather (1900), who had classified *Edriocrinus* “provisionally” as a flexible, because her specimens of *Edriocrinus* had at least one anal plate preserved. In Talbot’s view, the presence of an anal plate excluded *Edriocrinus* from the flexibles, whereas the modern definition of flexible crinoids includes the presence of at least one anal plate (Moore in Moore and Teichert, 1978). Although Talbot recognized that the *Edriocrinus* cup was similar to the cups of Family Cyathocrinitidae, now a cladid family, she concluded that too many differences existed to classify *Edriocrinus* in this family. These differences were the stemless nature of *Edriocrinus,* brachials, when preserved, that were wider than high, and an arm-branching pattern unlike that of the Cyathocrinitidae. Instead, she placed *Edriocrinus* in a family she designated within the same article, the Family Edriocrinidae Talbot, 1905, despite the earlier designation of the Family Edriocrinidae for the same genus (Miller, 1889). Talbot (1905, p. 22–23) described the genus as follows:

> "Calyx directly cemented, either throughout life or only in the young stages, the attachment being by the large infrabasals. The cicatrix very large in some specimens and in others obliterated, by the accumulation of calcareous matter on the outer surface of the calyx plates. Infrabasals large, their height being from one-half to two-thirds that of the cup as ordinarily found, completely fused so as to destroy suture lines and to make the number of plates uncertain. Basals five, height varying in proportion to that of the infrabasals, generally so fused as to show no suture lines on the outer surface, although they are often seen on the inner side. Upper margin scalloped for the attachment of the radials and the anal plate. Radials five, large, rectangular, the upper margin excavated slightly for the attachment of the brachials and the lower curved to fit into the concave upper margin of the basals. An anal plate half as wide as the radials and a small plate above it furnish all that is known of the anal area. Ventral surface unknown. Arms known only in one species, *E. sacculus*, where they consist of very short transverse plates and bifurcate several times, but show no trace of pinnules."

Kirk (1911) also disagreed with classifying *Edriocrinus* as a flexible, suggesting that it was classified as a flexible because no more appropriate subclass was available. From eight specimens, he also described a new stemless, attached, morphologically unique species, *E. dispansus,* which apparently lacked basal and infrabasal plates. He never made a direct statement of the presence or absence of basals and infrabasals among *E. dispansus*, but certainly implied their absence. Moreover, he implied that this species, and perhaps other *Edriocrinus* species, lived as epiplankton or attached throughout their lives like the stemless articulate genera *Cotylederma, Eudesicrinus,* and *Holopus* (Fig. 3.1A, B, C). Kirk also emphasized that all three of these genera lacked both infrabasals and basals and lived attached "by a solid calcareous disk." He inferred a similar lifestyle for *Edriocrinus.* However, his placement of *E. dispansus* in the genus *Edriocrinus* is unusual because of the strong agreement among previous workers that *Edriocrinus* at least had basal plates. Although Kirk apparently knew enough about *E. sacculus* to interpret its mobile lifestyle, it appears that most of his familiarity with the genus came from the literature. Even the type specimens of *E. dispansus* in the U.S. National Museum suggest that they were not collected by Kirk himself, but rather by Schuchert. Hence, it is possible that Kirk only had indirect knowledge of *Edriocrinus,* which may explain his rather inexact, even contradictory presentation of the genus. Furthermore, Kirk described the dorsal cup of *E. dispansus* as "amorphous" and noted a high degree of morphologic variation among members of the genus. He posited a spectrum of morphologic possibilities with *E. pyriformis* and *E. dispansus,* a flat, discoid species, as the endpoints. Kirk also suggested an ontogeny for *Edriocrinus* during which young *Edriocrinus* detached from most of the stem but retained a few of the proximal columnals. After an intermediate free-swimming stage, *Edriocrinus* became re-attached at maturity, and the few remaining columnals "coalesced" into "such structures as we find" (Kirk, 1911). He also suggested that some *E. sacculus* remained attached throughout their lives.

Ohern (1913) also reported two anal plates in the genus and noted that the arms of *E. sacculus* were usually broken. No known arms of *Edriocrinus* have ever been described as pinnulate. Only one year later, after examining additional specimens, Jaekel (1914) came to realize that *Lodanella* was not a cystoid but rather an edriocrinid crinoid related to *Edriocrinus.* He also believed that *Lodanella* should be classified within his Suborder Articulosa Jaekel, 1894, a taxon that he considered nearly equivalent to the Articulata Wachsmuth and Springer, 1886 (Jaekel, 1894, 1914). He also noted that, although they were related, *Lodanella* and *Edriocrinus* were distinct genera. Additionally, he found that *Edriocrinus* was related to the families Lecanocrinoidea, Taxocrinoidea, and Ichthyocrinoidea. All three are now families of the Flexibilia, but they were all formerly included in the Articulosa Jaekel, 1894. Wanner (1915) also recognized that *Lodanella mira* was a crinoid closely related to *Edriocrinus,* but he classified *Lodanella* in the flexible family Ichthyocrinoidea.

Five years later, Springer (1920) undertook the next major attempt to revise the genus. He was the first to recognize the taxonomic significance of the patelloid process in flexible crinoids, although Hall had first observed and named this structure (Ubaughs in Moore and Teichert, 1978). Springer (1920) described four new species of *Edriocrinus* based on his own material, *E. occidentalis* (~100 specimens)*, E. explicatus* (nine specimens)*, E. adhaerens* (three specimens)*,* and *E. holopoides* (21 specimens). He considered the unusual genus to be *incertae sedis* and noted that the monocyclic and nonflexible calyx prevented its classification with the flexibles. The lifestyle of a permanently attached basal cup was also unlike that of any other flexible crinoid. Springer also divided the genus into two main groups. The species that were unattached in adulthood included *E. pocilliformis, E. occidentalis, E. explicatus, E. dispansus, E. sacculus,* and *E. becraftensis,* whereas those that remained attached by the base in adulthood comprised *E. adhaerens, E. pyriformis,* and *E. holopoides.* The three attached species apparently adapted their bases to the shape of the attachment surface.

In stark contrast to Talbot (1905), with whom he strongly disagreed, Springer (1920) described the genus as monocyclic with only four, not five, basal plates. Strikingly, he did not directly compare any specimens of *E. pocilliformis* or *E. sacculus* with Talbot's (1905) interpretation. Instead, he justified his ideas based on the number of plate circlets below the radials and the number of plates in the circlet in each of the four species, *E. occidentalis, E. explicatus, E. dispansus,* and *E. adhaerens.* Three of these species were also described in his monograph for the first time. Also, unlike Talbot's specimens, none of these four species had any preserved arms. The two words he devoted to describing the arms could only have been based on the arms of *E. sacculus* and *E. holopoides,* another newly described species in his monograph; arms of all other described species remain unknown. His revised generic description follows:

> "Crinoids without stem; either permanently attached directly by the base, or free in the adult stage. Monocyclic; BB 4, fused into a more or less hollow mass (hereinafter simply called the base) with sutures usually obliterated by secondary growth. RR in contact all around except at the anal side. Anal plate in line with radials, usually projecting above their level. Radial facets filling distal face of radials. Arms dichotomous. Pinnules probably wanting (Springer, 1920, p. 443)."

Springer further contended, based on *E. adhaerens,* that six scalloped depressions (lines) present inside the preserved bases corresponded to five radials and one anal plate, because they divided the fossil into six parts. He argued that if the lines defining the depressions were interbasal sutures corresponding to five basals, as Talbot (1905) had reported, the cup should be divided into five parts. He did not suggest a stem had ever been present among any *Edriocrinus* at any point of life. Springer also wrote that the stemless, attached, flexible crinoid *Palaeoholopus* strongly resembled the Devonian genus *Edriocrinus* and the modern genus *Holopus*.

Regarding the species *E. adnascens,* Dunbar (1920) proposed a third family designation, the stemless family Agassizocrinidae, as it was known at the time. Among *E. adnascens*, he indicated that five radials and one anal must have been present and interpreted it to have been an attached form throughout life. Subsequently, Goldring (1923), like Springer (1920), stated that the monocyclic nature of the cup excluded *Edriocrinus* from the flexibles.

Ehrenberg (1928) reported a number of apparent morphologic similarities among species of the genus *Edriocrinus*. He believed that some juvenile specimens of described as *E. sacculus* could be specimens of *E. becraftensis*. Similarly, he believed that some young specimens of described as *E. sacculus* could be *E. holopoides*. Ehrenberg (1928) suggested these interpretations because he noted that most of the *Edriocrinus* bases (infrabasal-basal cones) available for study from these species resembled each other, especially those which reflected similar ontogenetic stages. Furthermore, Ehrenberg considered combining the four species, *E. pocilliformis*, *E. occidentalis, E. sacculus*, and *E. becraftensis*, because he found that they were not well-defined species. He ultimately concluded that of these four, *E. sacculus,* with its well-preserved arms and radials, was the best-defined, (though still inadequately so), as a species by itself, and that the other three species, lacking such preserved features, could not be combined. He also believed that too few differences existed among *E. pocilliformis, E. sacculus, E. becraftensis,* and *E. occidentalis* to justify their status as individual species.

Moore and Laudon (1943) agreed that *Edriocrinus* was not like other flexibles. They also noted that the similarity between the arms of flexibles and those of *Edriocrinus,* for which they described broad arms that branched isotomously, is the only rationale for classifying it with the flexibles. No other flexible crinoid was known to be monocyclic. Moore and Laudon wrote that if *Edriocrinus* were to remain with the flexibles, evidence of infrabasals that were reduced or possibly fused with other plate circlets was required. They deemed that the origin of *Edriocrinus* was uncertain, noted that juvenile *Edriocrinus* were attached directly by the base with no stem, that *Edriocrinus* had four fused basals, and that the anal X was in line with the radials.

LeMaître (1954) was the first to report *Edriocrinus* outside of North America, from Algeria, whereas Prokop (1976) reported and described the first European specimens designated as *Edriocrinus* from the Czech Republic. Strimple (1963) noted that *Lodanella* and *Edriocrinus* were related, and Strimple (1977) believed that *Edriocrinus* would show a worldwide distribution among Lower and Middle Devonian rocks. He also argued that the small basal circlets were frequently overlooked, and that the attached young could have been distributed as a result of their epiplanktonic lifestyle (Strimple, 1977). Strimple (in Moore and Teichert, 1978) suggested attachment directly by the base of the cup, without a stem, "at least during youthful stages (p. T812)." His generic diagnosis follows:

> "Cup thought to be pseudomonocyclic, i.e., infrabasals probably present in ontogeny but fused or resolved in process of producing base for attachment to foreign objects. Arms strikingly similar to those of flexible crinoids (in Moore and Teichert, 1978, p. T812)."

Later, Prokop (1995b) reported isolated plates of *Edriocrinus*, including radial plates, which showed evidence of straight radial facets and a muscular articulation. Also, Prokop and Petr (1995a) and Prokop and Turek (2014) reported evidence of five radial plates and one anal plate in the dorsal cup. Like Strimple (in Moore and Teichert, 1978), Seilacher and MacClintock (2005) reported juvenile attachment directly by the base, and they also suggested lifelong attachment if the shell was big enough to support continued growth of the crinoid. Donovan (2006) noted that the similarity between *Edriocrinus* and extant holopodids may include fused plates without visible sutures.

Hence, a summary of the taxonomic history of *Edriocrinus* shows that much of the confusion surrounding the classification and description of *Edriocrinus* has derived from interpretations based on the absence of a tegmen and pinnules, disagreement about the number and types of plate circlets, and a reliance on stemlessness to the exclusion of other characters. Thus, morphological taxobases were not consistent among previous workers. Furthermore, placement in the Superorder Flexibilia is based on the two species with preserved arms (*E. sacculus* and *E. holopoides*), which show the first primibrachial equal in width to the radial and arms resembling those of the flexible Family Lecanocrinoidea (Clement and Brett, 2015). A third criterion that has placed all of the species currently recognized in *Edriocrinus* within the same "genus" is their similar age of occurrence (Early–Middle Devonian). However, age cannot qualify as a morphological taxobasis. To illustrate the diversity of ideas on the genus, the original descriptions of each *Edriocrinus* species are reproduced herein.

Edriocrinus pocilliformis Hall, 1859

″Base hemispheric or subturbinate, often less than a hemisphere, externally smooth or finely granulate : upper margin scollopped with five large and one smaller depression for the insertion of the radial and anal plates. Interior more or less deeply concave, with depressions corresponding to those on the edge of the cup; the concavity not parallel to the exterior convexity. Radial plates and arms unknown (Hall, 1859, p. 121).”

Edriocrinus sacculus Hall, 1859

″Body more or less obconic or turbinate below and cylindrical above, varying in its proportions of length and breadth. Base varying in form from turbinate to hemispheric, solid, often obliquely truncate or indented below : upper margin marked by six subangularly concave depressions for the insertion of the radial and anal plates. Radial plates large, longer than wide, inserted into the depressions in the margin of the base, gradually expanding towards the upper margin which is thickened externally, slightly concave for the reception of the plates of the arm.

Arms broad at the base, composed of numerous very short transversely linear plates, of which ten or twelve or more occur below the first bifurcation : first bifurcation in the middle, and each side again bifurcating on the third or fourth plate above, with each division bifurcating once or twice beyond this; making eight or ten or more divisions at the extremities. Anal plates two, the lower large and of the same form as the radial plates; the second one small and short. Proboscis and summit unknown. Column none : affixed to foreign bodies by the solid base (Hall, 1859, p. 143—144).”

Edriocrinus pyriformis Hall, 1862

″General form elongato-pyriform or subclavate. Base elongate, subcylindrical, more or less attenuate, solid, or the plates closely anchylosed. Radial plates more rapidly expanding, giving a short turbinate aspect to the upper part of the body, contracting towards their superior margins, which are more or less abruptly bent inwards; the upper margins marked by two narrow grooves, for the insertion of the next series of plates. Surface smooth or finely granulose-striate (Hall, 1862, p. 116).”

Edriocrinus becraftensis Clarke, 1900

″The calyxes of this species may be distinguished from those of *Edr. sacculus* Hall from the Oriskany sandstone of Cumberland Md. in their elongate, much more slender and very gradually enlarging form, and generally quite small size. They are blunt but not broad at the base and enlarge upward with gently incurving sides. In one instance only has the upper edge of the calyx been observed, and except for this edge no specimen shows traces of the component plates. The casts of the calyx are not infrequent (Clarke, 1900, p. 62)."

Edriocrinus dispansus Kirk, 1911

"*Edriocrinus dispansus,* new species,…offers perhaps the most interesting variant from the normal *Edriocrinus* structure. In this species…the base is greatly expanded…Despite the great expanse of the lower portion of the cup, the diamater of the theca at the arm bases is comparatively small. It is to be noted that the radials and anal are directed inward, rather than vertically or outward, as in the case of most Crinoidea. As a result the radials are considerably broader at the base than at the top (Kirk, 1911, p. 112)."

Edriocrinus adnascens Dunbar, 1920

"Base flat and cemented to some foreign object, usually a brachiopod shell. The central portion is occupied by a broad and very shallow depression, bounded by a low rim, outside of which the surface is concave as it slopes away to the margin. The rim of the shallow basal cup is scalloped by six slight, concave depressions for the insertion of the five radials and the anal plate. Since these are all of the same size, the anal was doubtless of about the same width as the radials. These scallops continue to the center of the visceral cup as shallow, concave, radial depressions. Radials and brachials unknown.

There is considerable variation in the size and thickness of these crinoid bases, the height of the rim, and the proportionate size of the cup. Frequently the base is very thin, appearing as a mere circular ring, while in other cases, as in the specimen shown in Figure 3, it is thickened and spreads beyond the margin of the visceral depression.

Dimensions: Width of the base of the type specimen, 13 mm.; width of cup, 8 mm.; height of rim of base, 3 mm. Of another specimen: base, 14 mm.; cup, 12 mm.; height, 2.8 mm (Dunbar, 1920, p. 120—121)."

Edriocrinus occidentalis Springer, 1920

"A rather small species, known by the base only. Base small, elongate, broadly rounded at lower end, with thick wall enclosing an inversely conical tubular cavity which narrows downward, leaving the wall thickest at the lower part; often constricted below the radial facet and expanding again towards them. Height to width in average of 20 specimens showing all variations, about as 1 to .75; specimens varying in size from 8 to 20 mm. high, and from 6 to 14 mm. wide at the top (Springer, 1920, p. 449)."

Edriocrinus explicatus Springer, 1920

"A smaller form than the last one, known from the base only. Base subglobose, widening slightly upward, with basals but slightly modified by secondary growth and the sutures therefore observable. Height and width about equal, and specimens varying from 5 to 9 mm. each way (Springer, 1920, p. 449)."

Edriocrinus adhaerens Springer, 1920

"A very small species; only the fused base known. Base low, spreading more or less at the encrusting surface, enclosing a broad shallow cavity; wall thin. Height to width of base about as 1 to 2. Specimens ranging from 5 to 10 mm. in diameter. Maximum specimens are nearly as wide as minimum specimens of *E. dispansus* having the rounded base fully developed, thus making it improbable that this is the young stage of that species (Springer, 1920, p. 451)."

Edriocrinus holopoides Springer, 1920

"A large species, but smaller than *E. sacculus*, and with a shorter base; represented by the complete crown. Base low and broad, usually standing oblique to the surface of attachment; wall thin, enclosing a broad, bowl-shaped cavity not contracting downwards; expanding slightly towards the radials. Calyx and arms otherwise similar to those of *E. sacculus*, except that the arms are shorter and their inrolled cluster relatively not so wide. IBr 5 or 6, exceptionally 7 or 8. Height to width of base in average of 21 large and small specimens, about 1 to 1.25. Dimensions of maximum crown: 45 mm. high and 35 mm. wide at greatest expansion of arm cluster; calyx, 28 mm. high by 25 mm. wide at the arm bases; base, 17 mm. high by 19 wide; minimum crown, 8 mm. high by 7 mm. wide; minimum base, 4 mm. high by 6 mm. wide. Thus up to their maximum the specimens of this species range in size about like those of *E. sacculus,* but the latter becomes considerably larger (Springer, 1920, p. 452)."

Edriocrinus ata Prokop, 1976

"The preserved basal parts of cups in the form of a wide, low truncated cone with relatively robust walls. Basals completely fused so that their number is indeterminable. The basal plate of the cup is smooth, flat or slightly concave, imitating the surface of the object (a nautiloid shell?) to which the crinoid was attached. In the upper portion of the basal part of the cup, there is a wide, very shallow ventral cavity showing concentric striation of walls. The cavity is divided by low, rounded interradial ribs into six fields, which correspond in position to five RR of identical size and one narrower anal plate X. The height: width ratio is 1 : 5, the angle of walls ca. 45° (Prokop, 1976, p. 188).”

Edriocrinus tara Prokop, 1976

"Cylindrical basal parts of the cups with smooth, even or slightly concave, relatively massive walls. The basal plate is somewhat widened where it sets on the host shell. The width: height ratio is 2.5 to 3 : 1. Ventral cavity, circular in outline, is slightly lobate, deep and strikingly concentrically striated. It is divided by interradial, rounded but prominent ribs into six separate fields, which correspond to five equally wide RR and a narrower anal plate X (Prokop, 1976, p. 188—189).”

Edriocrinus cylindricus Prokop, 1976

"Cylindrical, mostly inclined basal part of the cup, consisting of completely fused BB. The walls relatively thin, smooth; basal plate flat, deformed according to the configuration of the host. The width: height ratio varies between 1 : 1 and 2 : 1. Ventral cavity also oblique-cylindrical, deep, smooth, circular or elliptic in outline, slightly lobate at the upper margin where RR were given off (Prokop, 1976, p. 190).”

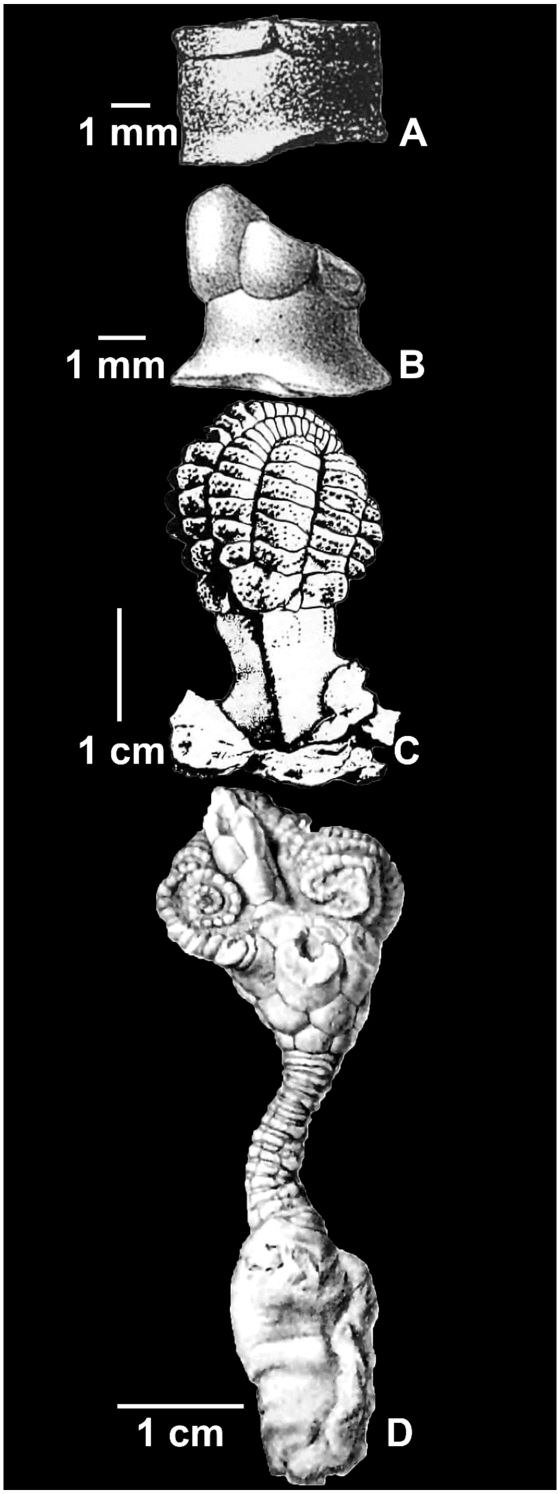

Figure 3.1. Similar arms and lifestyles to *Edriocrinus*. A: *Cotylederma,* a stemless, attached articulate. B: *Eudesicrinus,* a stemless, attached articulate. C: *Holopus,* a stemless, attached articulate showing similar arm structure to *Edriocrinus.* D: *Euspirocrinus,* now a eucladid, also showing similar arm structure to *Edriocrinus.* (A and C modified from Rasmussen in Moore and Teichert, 1978, B modified from Hess in Selden, 2011, D modified from Lane and Moore in Moore and Teichert, 1978).

CHAPTER 4. THE SUPERORDER FLEXIBILIA

Throughout its history, *Edriocrinus* has most commonly been classified within the crinoid Superorder Flexibilia. To understand why this classification is or is not appropriate for *Edriocrinus,* it is essential to first understand what a flexible crinoid is and the bases for classification therein.

4.1 Diagnostic characteristics of flexible crinoids

At every taxonomic rank, groups such as the Superorder Flexibilia (Zittel, 1895) Wright et al., 2017, the Family Edriocrinidae Miller, 1889, and the Genus *Edriocrinus* Hall, 1858*,* are based on distinct characters, or taxobases, shared by all organisms in their respective taxa. Significant flexible crinoid taxobases come from the articulations between the plates of the cup and the number and types of plates that constitute the cup (Moore and Laudon, 1943; Moore in Moore and Teichert, 1978). Within the cup, the radial articular facets of flexibles are unique among Crinoidea and distinguish them from camerates and cladids (Moore et al., 1952). Also, among camerates and most cladids, the entire joint faces of their calyx plates are flat and smooth, whereas those of the flexibles typically have crenulated rims (Fig. 4.1A) (Ubaughs in Moore and Teichert, 1978). Furthermore, the flexible crinoids share a conservative suite of important characteristics, namely, the occurrence of three infrabasals, no visible break in contour between the radials and the primibrachials, and uniserial, nonpinnulate arms (Moore and Laudon, 1943). These remarkably consistent characteristics were retained throughout the long geologic range of flexibles (Ordovician–Permian), which originated with the flexible genus *Protaxocrinus*

(Moore in Moore and Teichert, 1978) in Middle Ordovician time (Wright et al., 2017). The diagnostic characteristics of flexible crinoids are as follows.

- Infrabasal circlet slightly to completely covered by proximal columnal (Moore in Moore and Teichert, 1978) (Fig. 4.1B, C);
- Cup dicyclic (Moore et al., 1952); some genera cryptodicyclic (Ubaughs in Moore and Teichert, 1978) (Fig. 4.1B, C);
- Infrabasal circlet consisting of two larger plates and one smaller plate; infrabasals fused in some genera (ankylosis) (Moore et al., 1952); small infrabasal typically in right posterior ray (Moore in Moore and Teichert, 1978) (Fig. 4.1B, C, D);
- Anal x present in most genera (Moore in Moore and Teichert, 1978) (Fig. 4.1E);
- Anal sac absent (Moore et al., 1952);
- Interbrachials and interradials numerous to few or absent (Moore et al., 1952) (Fig. 4.1F, G, H);
- Tegmen flexible, consisting of exposed food grooves and mouth (Moore et al., 1952) (Fig. 4.1I);
- Brachials not rigidly attached to radials (Moore et al., 1952);
- Outline of crown showing no break between the radial circlet and the first primibrachial (Moore et al., 1952) (Fig. 4.1J);
- Two primibrachials in each ray of most genera, three in some genera, and four in even fewer genera (Moore and Laudon, 1943) (Fig. 4.1J);
- Brachials wider than high (Moore in Moore and Teichert, 1978) (Fig. 4.1J);
- Uniserial, non-pinnulate arms characterized by presence of patelloid process in most forms on aboral side (Springer, 1920) (Fig. 4.1J);

- Primitive arm branching isotomous; advanced arm branching may be isotomous or heterotomous; branching absent in a few highly evolved flexibles (Moore et al., 1952); in some forms, the main arm branch is isotomous and each secondary branch is heterotomous (Moore in Moore and Teichert, 1978) (Fig. 4.1K);
- Arms curled inward and tapered distally (Springer, 1920) (Fig. 4.1L).

The characters above are in sharp contrast with those present in the genus and species of *Edriocrinus*. A detailed discussion of the relevant taxobases of *Edriocrinus* and a revised rank-based classification follow.

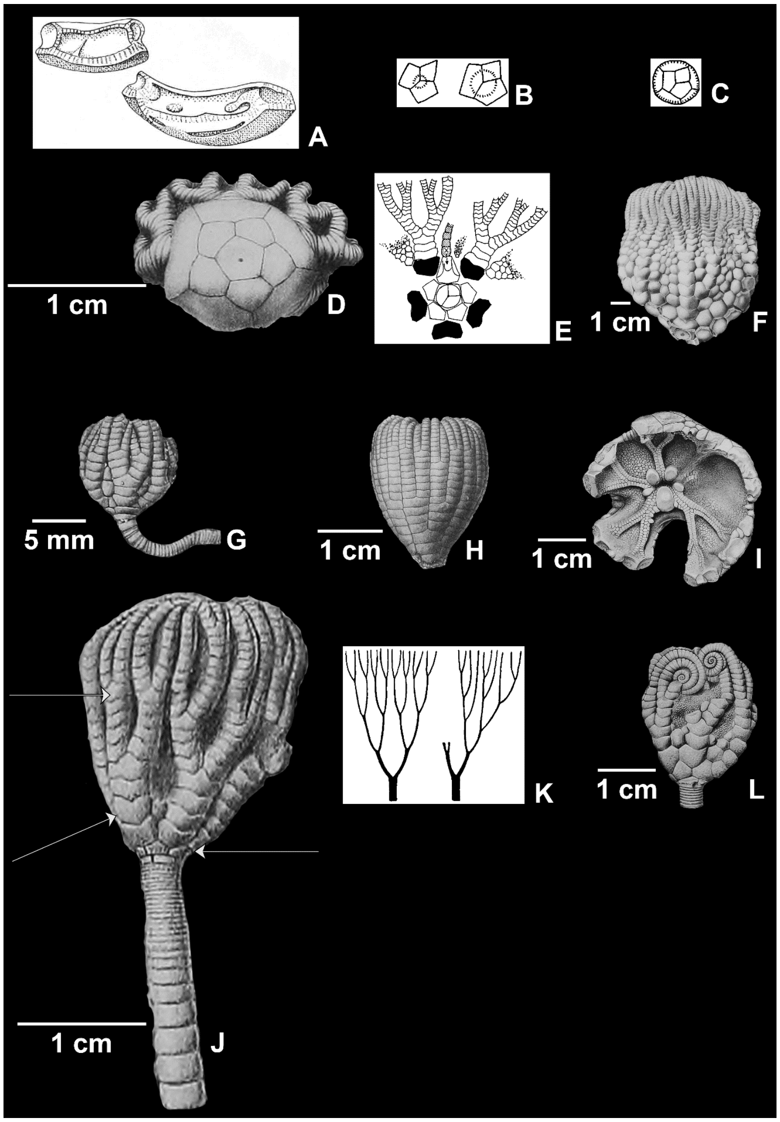

Figure 4.1. Characters of flexible crinoids. A: Crenulated rims of basal (top) and radial (bottom) of *Forbesiocrinus nobilis.* B: Stem, marked with hachure marks, slightly to somewhat covering infrabasals of unequal size. C: Stem, marked with hachure marks, completely covering infrabasals, thus creating a cryptodicyclic cup. D: *Nipterocrinus arboreus* showing fused infrabasals. E: Plate diagram of *Taxocrinus* showing anal plate, marked with X. F: *Forbesiocrinus agassizi* showing numerous interbrachials and interradials. G: *Homalocrinus parabasalis* showing few interbrachials and interradials. H: *Ichthyocrinus pyriformis* showing no interbrachials or interradials. I: Tegmen of *Taxocrinus intermedius.* J: *Taxocrinus communis* showing no break in the outline of crown (lowermost arrow), four primibrachials (center arrow), and brachials wider than high (topmost arrow). K: Isotomous arm branching (left) and heterotomous arm branching (right). L: Arms of *Temnocrinus tuberculatus* curled inward and tapered distally. (A and K modified from Ubaghs in Moore and Teichert, 1978. B, C, E modified from Moore in Moore and Teichert, 1978. D, F, G, H, I, J, and L modified from Springer, 1920).

CHAPTER 5. REVISED SYSTEMATICS OF *EDRIOCRINUS*

Phylum Echinodermata

Class Crinoidea Miller, 1821

Subclass Pentacrinoidea Jaekel, 1894

Infraclass Inadunata Wachsmuth and Springer, 1885

Parvclass Cladida Moore and Laudon, 1943

Magnorder Eucladida Wright, 2017

Superorder Cyathoformes Wright et al., 2017

Order ‘Dendrocrinida’ (Bather, 1899) Wright et al., 2017

Superfamily ?Merocrinacea S.A. Miller, 1890

Family Edriocrinidae S.A. Miller, 1889 (*non* Edriocrinidae Talbot, 1905)

Genus *Edriocrinus* Hall, 1858

Type species. — *Edriocrinus pocilliformis* Hall, 1859, by subsequent designation and position precedence

Diagnosis.— Dicyclic crinoids, stemless and appearing pseudomonocyclic in maturity; visible parts of cup largely composed of basal and radial plates, enhanced by deposition of laminar calcite; arms, where preserved, raptorial, flat, strip-like, uniserial, non-pinnulate, with very short, broad, rectilinear brachials.

Description. — Dicyclic eucladid crinoids; aboral cup low–high, conical–bowl shaped, and its shape may be a cup, cone, or disk, becoming stemless and mostly cryptodicyclic in mature stages. In immature stages, infrabasals (IBB), basals (BB), and radials (RR) mostly visible from side unless cup is discoid. At maturity, five IBB become concealed or may remain visible from side and grow by encapsulating proximal stem fragment, the circular, central, occasionally impressed, outline of which may be visible internally, or externally on some abraded individuals; in some species, IBB merge into a thick, heavy cone of calcite around proximal stem fragment; IBB may be mostly external in immature forms; internal cavity of cup or IB-B cup, cone, or disk shallow to deep, or absent. Five BB externally overgrow or subsume all or parts of IBB by deposition of laminar calcite below R circlet to form a fused IB-B cup, cone, or disk, which in some species may be directly cemented to the substrate, thereby creating a pseudomonocyclic appearance. Uppermost margin of BB may flare outward and is at least partly scalloped for reception of RR and radianal (RA). Five RR in contact except at radianal (RA) (sensu Wright, 2015); R facets projecting outward on lip-like flanges; facets declivate or planate, all are plenary and muscular. RA is the only anal plate in cup, in line with RR but narrower than RR, projecting above RR. First primibrach (PBr$_1$) broad and short, at least equal in width to RR; in one species, PBrBr 4–17 axillary. Where preserved, five flat, strip-like, uniserial, proximally isotomous, distally heterotomous, nonpinnulate arms with very short, broad, rectilinear brachials (BrBr) and prominent V-shaped adoral groove; arms typically enrolled distally; tegmen and anal sac unknown in all species.

Occurrence. —Ulsterian (Early–early Middle Devonian; middle Lockhovian–early Eifelian; ~416.2 Ma?–~391 Ma). (*Ancyrodelloides carlsi–Polygnathus costatus* conodont zones), United States, Germany, Algeria, Czech Republic, England.

Remarks. — The laminar cup of *Edriocrinus,* which is unique among crinoids, developed outwardly as the IBB and BB merged and the BB grew downward to various degrees to encapsulate the IBB. Consequently, the extent of encapsulation varies among individuals of the same species and even their single plates. All may appear remarkably different from each other. Many individuals are only known from IB-B cones, cups, or disks, which previous workers frequently called the base or basal circlet (Hall in Silliman et al., 1858, Hall, 1859, 1862; Meek and Worthen, 1868; Wachsmuth and Springer, 1879, 1885, 1886; Miller, 1889; Keyes, 1894; Bather, 1900; Schuchert, 1905; Grabau and Shimer, 1910; Ohern, 1913; Jaekel, 1914; Dunbar, 1920; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Clement and Brett, 2015). Furthermore, many specimens show unequal cup development on different sides of any one specimen, whereas others may show their true dicyclic nature only when basals have been weathered away from infrabasals or the growth of basals was incomplete before death. Also, mature *Edriocrinus* lived cemented to the substrate or lived an unattached, epifaunal or semi-infaunal lifestyle on the bottom. Therefore, the intraspecific variations among disks, cups, and cones may reflect bottom environmental conditions, such as abrasion by high-energy moving sands, and ecophenotypic variations in cup shape adapted for dynamic conditions. Such small intraspecific variations, however, are probably not significant enough to be taxobases but have been interpreted as such by many previous workers.

Regarding arms, only some individuals of one species, *E. sacculus,* retained preserved arms, which are incurved distally to widely varying degrees. *Edriocrinus* has been considered *incertae sedis* within the Flexibilia since 1900 without much consideration of the cup primarily because of the inward coiling arms (Figs. 5.2B, D, E, G, I, 5.3A, B, D, E, F, H), although such coiling is not exclusively known among flexibles (Ubaghs in Moore and Teichert, 1978). However, *Edriocrinus* tends to show a distinct break in the calyx outline between RR and PBr$_1$, with arms free above RR, in stark contrast to the flexible crinoids. Furthermore, the large size of the cup relative to the arms, presence of five, high IBB visible from the side at least in juvenile stages, the absence of a patelloid process, and especially the muscular nature of the radial articular facets justify the removal of this genus from the Flexibilia and placement within the Eucladida.

More broadly, Eucladida is a part of the Subclass Pentacrinoidea (Wright et al., 2017). The defining characters of most clades commonly have exceptions, variations, and additions to the characters given herein, which only include the characters most relevant to *Edriocrinus,* because of the diversity and long geologic range of crinoids. In any case, pentacrinoids have posterior plates proximal to the C-ray radial plate; calyx plates somewhat rigidly united; "a non-rigid to flexible oral region;" and an exposed mouth (Wright et al., 2017). Because *Edriocrinus* shows these characters, it is also a pentacrinoid. Within the Subclass Pentacrinoidea, the Infraclass Inadunata is characterized by free arms above the radials (Wright et al., 2017), like those of *Edriocrinus*; so, it is a member of the Infraclass Inadunata.

The Infraclass Inadunata includes the Parvclass Cladida. The Cladida are dicylic; typically have posterior plates, which may be lost or retained through adulthood, characteristically positioned below and/or in line with the radial plates; and Middle Paleozoic to Recent Cladida often tend to be pinnulate, except for the flexibles (Simms and Sevastopulo, 1993; Wright, 2015; Wright et al., 2017). Likewise, *Edriocrinus* was a dicyclic crinoid with the RA in line with the RR during adulthood, suggesting that it is also a member of the Cladida.

A part of the Parvclass Cladida is the Magnorder Eucladida. Characters of the Eucladida include dicylic calyces; dorsal cup plates which are tightly bound together; free arms above the radials; and subtegminal mouths (Moore and Laudon, 1943; Wright et al., 2017). The taxonomically significant arm facets are muscular (e.g., Van Sant and Lane, 1964; Ubaghs in Moore and Teichert, 1978) with a transverse ridge that may be prominent, unlike the ligamentary arm facets of the flexibles (Ubaghs in Moore and Teichert, 1978). Moreover, the patelloid process indicates a ligamentary articulation, whereas the BrBr of *Edriocrinus* are joined by muscular articulations. Because the cups and arms of *Edriocrinus* species show most of these characters, where preservation allows, it is likely a eucladid crinoid.

The Magnorder Eucladida includes the Superorder Cyathoformes Wright et al., 2017. Characters of the Cyathoformes include dicyclic calyces; crown and cup of highly variable size and shape; infrabasals five, three, or fused into one solid circlet and visible from the side unless the base of the cup is flat or concave; five-to-zero anal plates in the cup, which may be visible from the side; an anal sac present or not evident; radial facets muscular or ligamentary; arms which are isotomous or heterotomous, with or without pinnules, and may bear ramules; brachials which may be uniserial or biserial; and a transversely round stem (Moore and Laudon, 1943; Lane and Moore in Moore and

Teichert, 1978; Moore, Lane, and Strimple, in Moore and Teichert, 1978; Moore, Strimple, and Lane in Moore and Teichert, 1978). Most of these characters are typical of *Edriocrinus,* meaning it is likely a part of the Superorder Cyathoformes.

An order within the Superorder Cyathoformes is the Order Dendrocrinida. Dendrocrinid characters include a moderately large crown; five IBB, possibly approaching fusion, that are mostly visible from the side unless the base of the cup is flat; three-to-no anal plates in the cup, which are visible from the side; anal sac and tegmen absent or poorly developed; preserved arms that are few, atomous, isotomous, or heterotomous, and typically nonpinnulate; uniserial BrBr that are typically rectangular; and a stem that is largely circular in cross section (Moore, Lane, and Strimple, in Moore and Teichert, 1978). Because *Edriocrinus* displays most of these characters, it is likely a dendrocrinid. Also, the Superorder Cyathoformes is based on phylogeny, defined by patterns of shared common ancestry, not by specific characteristics (Wright et al., 2017). Herein, placement of *Edriocrinus* within the Order 'Dendrocrinida' is based wholly on the similarity of its characters to those as presented by Moore, Lane, and Strimple (in Moore and Teichert, 1978).

Some crinoids of the Order 'Dendrocrinida' are included within the Superfamily Merocrinacea. This superfamily is characterized by five IBB, which are visible from the side unless the base of the cup is flat and upflared to varying degrees; large BB; and large RR. Most members of this superfamily have three anal plates in the cup; lack fixed BrBr, interbrachials, and interradials; have uniserial, nonpinnulate arms with one-to-many PBrBr; arms which are isotomously branched proximally, sometimes becoming heterotomous distally; and a transversely circular stem. This combination of characters suggests that *Edriocrinus* is probably best placed herein. On the other hand, the fusion and lamination of the IBB and BB; single anal plate in the cup; and absence of an anal sac (e.g., Moore and Lane in Moore and Teichert, 1978) suggest the genus may be distinct from other merocrinacean families and warrants its own family. Therefore, *Edriocrinus* is retained within its own family, the Family Edriocrinidae S.A. Miller, 1889 (*non* Edriocrinidae Talbot, 1905).

The genus is also distinctive among crinoid genera because the possible overgrowth of the early stem by IBB, overgrowth of all or parts of the IBB by BB, and outward growth of the cup below the level of RR occur by accretion of laminae, although laminae may be obscured by poor preservation. The five BB may have varying degrees of internal and external expression, and their external visibility may differ, even among each of the BB on individuals. These BB encapsulate and sit atop the IBB and/or may be recessed within a hollow on the adoral surface of the IBB. This relationship between the IBB and BB and growth by addition of laminae are unique among crinoids. Therefore, *Edriocrinus* is retained within its own genus.

Edriocrinus pocilliformis Hall, 1859

Figure 5.1

1859 *Edriocrinus pocilliformis* Hall, p. 121, pl. V, figs. 8–12.

1905 *Edriocrinus pocilliformis*; Talbot, p. 20–23, pl. IV, figs. 1–6.

1920 *Edriocrinus occidentalis* Springer, p. 445, p. 449, pl. LXXVI, figs. 6–12.

1920 *Edriocrinus explicatus* Springer, p. 445, p. 449, pl. LXXVI, figs. 13–15.

1923 *Edriocrinus occidentalis*; Goldring, text fig. 61a.

1923 *Edriocrinus explicatus*; Goldring, text fig. 61b.

1928 *Edriocrinus explicatus*; Ehrenberg, pl. VII, fig. 10.

1928 *Edriocrinus occidentalis*; Ehrenberg, pl. VII, figs. 12a–c.

2015 *Edriocrinus occidentalis*; Clement and Brett, p. 70, pl. 11, fig. 10.

1978 *Edriocrinus pocilliformis*; Ubaghs in Moore and Teichert, fig. 70,12.

2015 *Edriocrinus explicatus*; Clement and Brett, p. 69, pl. 11, figs. 4–5.

Holotype. —Cotypes, infrabasal-basal cups, (AMNH 35121–35123) from the Devonian New Scotland Formation, Helderberg Mountains, Albany County, New York.

Diagnosis. —Dorsal cup small, unattached. BB developed on internal IB shelf, mostly internal with smaller external expression as a fused B ring. Arms and tegmen unknown.

Description.— Dorsal cup small, conical to bowl-shaped (Fig. 5.1C, E), 11–22 mm high, may show unequal development on different sides of any one specimen, particularly of IBB and BB; maximum width at the level of RR, 7–19 mm wide, but may be asymmetrical; base of cup formed of fused IBB and BB (Fig. 5.1A), which may be truncated by abrasion. IBB wholly external in immature forms; IB-B cones conical to bowl-shaped and may be truncated; plates in cup are thick, smooth, and slightly tumid and may extend outward at adoral plate margins with lip-like flange; some cups constricted just below the flange or dorsal margin (Fig. 5.1E); sutures scalloped and slightly depressed. Stem apparently round and only present in immature stages and lost at maturity; overgrown or abraded possible stem attachment scar present in some individuals but often acentric (Fig. 5.1F). Five IBB, diamond-shaped with nearly flat adoral surfaces on which BB rest; IBB merge into a thick, heavy cone of calcite as IBB encapsulate proximal stem fragment; interior adoral surface of IBB forms a shallowly dipping, scalloped shelf around a deep, circular central impression that may reflect an encapsulated stem fragment; depression may be acentric (Fig. 5.1D, E, I). BB exhibit differing internal and external expressions, but may be largely internally developed on IB shelf; BB expand upward and outward to form a low external expression one-half to one-sixth the height of IBB; BB typically flare outward enough to form a slight lip above IBB, and uppermost margin of BB may flare outward; BB may merge adorally to effectively form a thickened B ring, sometimes incompletely expressed, above the level of IBB; BB grow downward around IBB to encapsulate all or part of IB cone (Fig. 5.1A). Fused IB-B cone grows outwardly by addition of calcite laminae around entire cone (Fig. 5.1H). Sutures between BB and RR slightly scalloped. Five pentagonal RR, higher than wide; sutures in R circlet straight and slightly depressed; RR in contact all around except at RA; RR and RA lack laminae of IBB and BB. R articular facet projects outward on a lip-like projection of adoral margin of R plate, declivate, plenary, with muscular articulation. One RA in line with RR, higher than wide, narrower than RR, but projecting adorally above level of RR. First primibrach (PBr$_1$) broad, short in height but equal in width to RR. Arms and tegmen unknown.

Remarks. — Compared to the other *Edriocrinus* species, this smaller form with a more compact cup is the only species to show the flattened IB shelf on the adoral surface of the IBB, upon which the BB rest (Fig. 5.1D). Most of the specimens show unequal development, particularly of the IBB and BB, on different sides of any one specimen. The most proximal parts of many specimens are abraded, revealing their true dicyclic nature as the BB are weathered away from the IBB or the growth of the BB was incomplete before death. When parts of the BB are missing, parts of the five IBB may still be visible, and BB which are complete and intact may entirely conceal the IBB, causing specimens to appear monocyclic (Fig. 5.1A, G). Any population may include individuals with and without visible IBB, like Talbot's (1905) specimens. Hence, she suggested that some of her specimens (of *E. pocilliformis*) were monocyclic and others dicyclic; nonetheless, she considered all of her specimens to be *Edriocrinus*. Therefore, Talbot (1905) suggested the presence of IBB in *E. pocilliformis,* but no previous literature discusses the attributes of the IBB, including the IB shelf, encapsulation of the stem by the IBB, and the overgrowth of the IBB by the BB. Although some researchers (e.g., Wachsmuth and Springer, 1886; Talbot, 1905; Springer, 1920) described the radial articular facets as plenary, none described their taxonomically significant muscular features.

In contrast to Talbot (1905), Springer (1920) believed that all *Edriocrinus* were monocyclic with four BB (Fig. 5.1B, C), and indeed, many specimens appear monocyclic as previously noted, regardless of their species or the true number of preserved plate circlets, because the BB eventually overgrew the IBB. Naturally, specimens he designated as *E. occidentalis* and *E. explicatus* are represented by the fused IB-B cones, not simply the B circlets. Among these IB-B cones, the internal part of a single specimen of *E. occidentalis* appears to have four divisions (Fig. 5.1B), which Springer (1920) believed to represent the sutures between four BB. Although the origin of this division exhibited by one specimen of *E. occidentalis* is unknown, it may have been teratological or taphonomic. In any case, this individual crinoid specimen does not definitively demonstrate that every "*E. occidentalis*" or every *Edriocrinus* had four BB, because evidence from better-preserved *Edriocrinus* specimens indicates that all species have five BB by definition. All known specimens of *E. occidentalis* are so poorly preserved by silicification that external plate boundaries are no longer evident, so discerning IBB from BB is difficult. Nevertheless, it is certainly possible that the BB are elongate as Springer indicated, particularly when the downward growth and encapsulation of the IBB were complete. The bases of some *E. occidentalis* are unusually thick (Fig. 5.1E), which may be the result of the growth process of encapsulation of the stem by the IBB and overgrowth of the IBB by the BB, combined with the thick deposit of calcite at the base of some *Edriocrinus* cups and cones. The constriction and expansion of the uppermost parts of the IB-B cones may be related to a B ring, or it may be an ecophenotypic trait associated with a soft substrate as noted in the discussion herein. Springer (1920) otherwise accurately noted slight variations in size and shape, but such variations are expected within any given species and should not be regarded as diagnostic of a separate *Edriocrinus* species. Moreover, the form and size of *E. occidentalis* specimens are similar overall to *E. pocilliformis*. Most importantly, where preserved, *E. occidentalis* shows the IB shelf, which is only known from *E. pocilliformis*, so the two "species" are likely the same and should be synonymized (Fig. 5.1E, I).

Regarding *E. explicatus,* Springer (1920) asserted that the lowermost, external elements of his nine cotypes of the fused IB-B cones of *E. explicatus*, which were collected from a single locality, show a division into four parts (Fig. 5.1C). Springer interpreted this as additional evidence for the sutures between four BB. However, IB-B cones of some of the nine specimens may be partly concealed by rock matrix (Fig. 1.4F), excessively prepared (Fig. 5.1B), or post-depositionally deformed, rendering determination of the true number of plates present difficult. Nonetheless, Springer (1920) erected *E. explicatus* based largely on the presence of four IB-B plates among his few cotypes. He also considered *E. explicatus* to be a distinct species based on the smaller size and subglobose shape of the IB-B cones, the slight distal expansion of the BB, and the absence of a constriction in the uppermost parts of the BB. Like *E. occidentalis*, Springer (1920) differentiated *E. explicatus* from other *Edriocrinus* species based on minor variations in cup shape and size, whereas we have found a much greater range of variations within some individual, larger specimen lots of *E. pocilliformis* than within Springer's nine cotypes. Thus, the same assertions outlined above for *E. occidentalis* also apply to *E. explicatus*. Above all, the IB shelf seen in some *E. explicatus* specimens, which is characteristic of *E. pocilliformis*, suggests that *E. explicatus* is a junior synonym of *E. pocilliformis.*

Edriocrinus sacculus Hall, 1859

Figures 5.2, 5.3

1859 *Edriocrinus sacculus* Hall, p. 143–144, pl. 87, figs. 1–22.

1885 *?Lodanella mira* Kayser, p. 207–213, pl. XIV, figs. 1–6.

1899 *?Lodanella mira*; Jaekel, p. 404–405.

1900 *Edriocrinus becraftensis* Clarke, p. 62, pl. 9, figs. 12–13.

1900 *?Lodanella mira;* Schlüter, p. 179, first unnumbered figure.

1911 *Edriocrinus sacculus*; Kirk, p. 112–113, pl. 11, figs. 14–15.

1913 *Edriocrinus sacculus*; Ohern, p. 11, pl. XL, figs. 7–12.

1914 *?Lodanella mira*; Jaekel, p. 382–385, figs. 1–4.

1915 *?Lodanella mira*; Wanner, p. 81–87, fig. 1.

1920 *Edriocrinus holopoides* Springer, p. 446–447, p. 452, pl. LXXVI, figs. 22a–b, figs. 23a–b.

1920 *Edriocrinus becraftensis*; Springer, p. 451.

1923 *Edriocrinus sacculus*; Goldring, p. 448–451, pl. 58, figs. 1–8.

1923 *Edriocrinus becraftensis*; Goldring, p. 453, pl. 58, fig. 18.

1923 *Edriocrinus holopoides*; Goldring, p. 455–456, text figs. 63a–d.

1928 *Edriocrinus becraftensis*; Ehrenberg, pl. VII, fig. 11.

1941 *?Lodanella mira*; Schmidt, text figs. 52a–b.

1944 *Edriocrinus sacculus*; Shimer and Shrock, p. 205, pl. 79, figs. 27a–b.

1978 *Edriocrinus sacculus*; Strimple in Moore and Teichert, fig. 548,1a.

1984 *?Lodanella mira*; Ettensohn, fig. 1.

Holotype. —Cotypes, infrabasal-basal cups, aboral cups, and crown (AMNH 35150–35165) from the Devonian Oriskany Sandstone, Cumberland, Allegany County, Maryland.

Diagnosis. —Dorsal cup sack-shaped, large specimens largest of all *Edriocrinus* species, 10–45 mm long, 10–40 mm wide, may be truncated by abrasion. IBB apparently encapsulate proximal portions of stem and may be overgrown by BB. Fused IB-B cone in dorsal cup lacks adoral IB shelf area but has laminae and prominent vertical striations or indentations. Five broad, strip-like, nonpinnulate arms, lacking patelloid processes, proximally isotomous, becoming heterotomous distally, slightly curving inward and bearing narrow, very deep adoral groove; BrBr broad, flat, short, and uniserial rectilinear.

Description. —Dorsal cup small to large; mostly conical (Fig. 5.3D) but can be variously shaped from medium-low bowl or high to nearly flat globe-shaped (Fig. 5.2C) or thimble-shaped; shapes may reflect truncation of base by abrasion; cup 10–45 mm high, 10–40 mm wide, commonly elongate elliptical along C-E axis (Fig. 5.3I), and may show unequal development on different sides of any one specimen; maximum width at the level of RR, and external cup outline in ventral view may also be round or asymmetrical, but IB-B cup interior has a distinctly angular aspect defined by 4–12 apparently random striations or linear indentations that run from adoral margin of BB downward (Fig. 5.3I); base of cup formed of fused or partially fused IBB and/or BB (Fig. 5.2H, J), which may be truncated nearly flat by abrasion. IB-B cones conical to bowl-shaped. Plates in cup are thick, smooth, and slightly tumid, possibly transected by anastomosing pores in some specimens (Fig. 1.4E); sutures externally scalloped, slightly depressed, and may be inwardly stepped between B and R circlets (Fig. 5.2E, 5.3D, E). Stem apparently round and only present in immature stages but lost at maturity; overgrown or abraded possible stem attachment scar present in some individuals but not always centered; IBB may encapsulate proximal parts of the stem, which may be visible internally, or externally on severely abraded individuals (Fig. 5.2H, J, Fig. 5.3C). Five IBB, elongated-diamond-shaped, higher than wide, merged to form a thickened accumulation of calcite, which is thicker at the base, commonly surrounding proximal stem fragment; lowermost part of inner cup shows deep, circular central impression that may reflect an encapsulated stem fragment; depression may be acentric. BB hexagonal and may merge downward with or overgrow IBB forming fused, laminated IB-B cone (Fig. 5.2A), eventually encapsulating IBB, but IBB possibly external in immature forms. BB equal to or slightly higher than IBB; uppermost margin of BB may flare outward; sutures between BB and RR slightly scalloped (Fig. 5.2E). Five pentagonal to nearly rectangular RR (Fig. 5.2E, 5.3D), generally wider than high; sutures in R circlet straight and slightly depressed; RR in contact all around except at RA (Fig. 5.3D). One anal plate in cup; RA in line with RR, higher than wide, narrower than RR; at least one other anal plate subequal in width to RA, present outside of cup (Fig. 5.3D). R articular facet projects outward on a lip-like projection of adoral surface of RR, plenary, planate to declivate, with straight muscular articulation bearing transverse ridge, ligament pit, and ligament pit furrow. Five broad, strip-like, nonpinnulate, uniserial arms with very prominent, narrow, V-shaped adoral groove, 6–10% of width of arms (Fig. 5.2B, D, E, G, I, Fig. 5.3A, B, D, E, F, G, H). Arms isotomously branched proximally, but specimens of *Lodanella mira*, herein synonymized with *E. sacculus*, become heterotomous distally, showing up to seven brachitaxes (Fig. 5.3G). Arms typically project outward above R facet, resting on a small shelf or outer marginal ridge, but subsequently recurve slightly inward (Fig. 5.2B, E, G, I, Fig. 5.3D, E, F). BrBr broad, flat, very short, and uniserial rectilinear, with a prominent V-shaped adoral groove, laterally lined on left and right with high adambulacrals (Adambamb) and lower, adradial rows of ambulacrals (AmbAmb); one side of groove with an uplifted shelf that may have supported cover plates (Fig. 5.3F). PBr$_1$ is broad, short in height but equal in width to or appears to exceed width of RR (Fig. 5.3D). PBrBr 4–17 axillary (Fig. 5.3G); perforate? BrBr united by muscular articulations (Fig. 5.2F); patelloid processes absent. Tegmen and anal sac unknown.

Remarks. — Internal vertical indentations from the BB downward are only evident in *E. sacculus,* including Kayser's (1885) German *L. mira* specimens, but their origin is unknown (Fig. 5.3I). Although the IB-B cones of all *Edriocrinus* species show a laminated construction, the laminae of both internal and external parts of the IB-B cones of *E. sacculus* are especially striking in appearance (Fig. 5.2A). In contrast to *E. pocilliformis, E. sacculus* has at least one other anal plate outside of the cup (Fig. 5.3D). Regarding the arms, the outward and subsequent inward nature of the curve apparently has no taxonomic significance, whereas the muscular R facets provide a firm taxobasis. The BrBr may have an angled, or stepped, appearance suggesting that the BrBr may have been capable of lateral motions (Fig. 5.3E).

Arms are only known from a few individuals, including the European species initially designated as *Lodanella mira.* Preservational artefacts from silicification that appear to represent the internal molds of small tubular channels, with intervening empty spaces, were interpreted as original morphological features (Fig. 1.4E). Therefore, *L. mira* was believed to be a sponge, a cystoid, and a crinoid capable of floating and swimming (Kayser, 1885; Jaekel, 1899, 1914; Schlüter, 1900; Wanner, 1915). The channels appeared to connect internal organs with the exterior of the cone, and these were thought to be similar to the pores that transect the walls of sponges (Kayser, 1885) or to the pore rhombs of cystoids (Jaekel, 1899). Similarly, Wanner (1915) believed that the intervening empty spaces within the plates meant that the cup of *Lodanella* was light enough to float, but nearly all workers rejected this idea. It is possible that some of the small channel molds represented original channel-like structures in life, even though examination of many specimens also indicates that some of the molds are, in fact, preservational artefacts.

However, as noted above, workers ultimately accepted that *L. mira* should be classified as a crinoid, and Jaekel (1914) rejected the possibility of floating or swimming.

Several researchers (Jaekel, 1914; Wanner, 1915; Ehrenberg, 1928; Ettensohn, 1984) have also agreed that *Edriocrinus sacculus* and *Lodanella mira* have many similarities. Descriptions since the earliest appearance in the literature, before *L. mira* was understood to be a crinoid (Kayser, 1885), consistently illustrated a resemblance to *Edriocrinus.* For example, the dimensions of some *L. mira* individuals which lack preserved arms (Kayser, 1885; Jaekel, 1899) are somewhat aligned with the dimensions of *E. sacculus.* Kayser's (1885) specimens are steinkerns and internal molds, and these modes of preservation have made the presence or absence of particular plate circlets uncertain. In this light, direct comparison with better-preserved *E. sacculus* is impossible. Like unattached *E. sacculus,* complete and partial cups of *L. mira* are thickly plated, proximally thickened, internally striated, and become thinner distally (Kayser, 1885; Jaekel, 1899, 1914; Schlüter, 1900; Wanner, 1915). Many specimens from Germany and England (Green and Sherborn, 1906) may be rather large but are likely incomplete and include only the IB-B cones (Jaekel, 1899, 1914; Schlüter, 1900; Green and Sherborn, 1906; Wanner, 1915). Nonetheless, they are cup-shaped, conical, or thimble-shaped (Jaekel, 1899; Schlüter, 1900) and plate boundaries generally are not visible below the RR (Kayser, 1885; Jaekel, 1899, 1914; Wanner, 1915) as is true of *E. sacculus.* Similarly, some specimens of *L. mira* lack evidence of an attached lifestyle (Jaekel, 1914; Wanner, 1915). In a few cases, *Lodanella* individuals have been interpreted to show limited evidence of IBB or BB (Jaekel, 1899, 1914). Some workers agreed that although the IBB and BB of *L. mira* are difficult to distinguish and that the BB may be absent or fused with the IBB, the typical growth of stemless crinoids suggests that a proximal stem fragment, IBB, and BB are represented even when lower portions of the cup appear smooth (Jaekel, 1914; Wanner, 1915). Above the BB, the RA is in line with low, tumid RR which are wider than high (Jaekel, 1914; Wanner, 1915). The sutures between the BB and RR, as well as the distal edges of the RR, both appear scalloped (Wanner, 1915). Notably, the outline of the calyx is sharply broken between the BB and RR and between the RR and PBrBr$_1$ (Fig. 5.3E) (Wanner, 1915). The straight interradial sutures are depressed, and the R facets are nearly identical to those of *Edriocrinus* with a transverse ridge (Wanner, 1915). Jaekel (1914) believed that *Lodanella* also had an anal tube. Although subsequent workers acknowledged the presence of an anal tube with a specimen of *Lodanella,* all agreed that it was originally part of a different crinoid preserved fortuitously close to the *Lodanella* specimen in the same rock unit (Wanner, 1915; Ehrenberg, 1928). Furthermore, Ehrenberg (1928) contended that if *Edriocrinus* lacked an anal tube, then the considerably similar *Lodanella* also lacked an anal tube. Regarding the preserved arms, they are isotomously branched proximally at PBr$_5$ax, becoming heterotomous distally (Jaekel, 1914; Wanner, 1915) like the arms of *E. sacculus.* The robust BrBr are very short, much wider than high, and all nearly equal in height with a prominent adoral groove (Schlüter, 1900; Jaekel, 1914; Wanner, 1915). The proximal BrBr are broad and low (Schlüter, 1900; Jaekel, 1914) with PBr$_1$ about 10 times wider than high (Wanner, 1915). Additionally, SBrBr are nearly half as wide as PBrBr (Schlüter, 1900; Wanner, 1915), so the BrBr of *L. mira* and *E. sacculus* are identical overall. All the characters of *L. mira's* arms are closely similar to those of *E. sacculus.*

Ultimately, workers since Jaekel (1914) have long understood that *L. mira* is a crinoid. Furthermore, they have considered it to be closely related to *Edriocrinus* because of commonalities in the shapes of cups and arms, as well as the similar ages, with the possible exception of *E. pyriformis* (Jaekel, 1914). The primary similarity has also been understood to be between *L. mira* and *E. sacculus* (Wanner, 1915; Ehrenberg, 1928). Despite many early workers' (Jaekel, 1914; Wanner, 1915; Ehrenberg, 1928) lucid grasp of the similarities between *L. mira* and *E. sacculus,* they remained hesitant to synonymize the two forms. Nevertheless, we interpret the two forms as the same. Therefore, *L. mira* is synonymized with the earlier name, *Edriocrinus sacculus.*

In contrast to *Lodanella mira,* morphologic data regarding the unattached species (Springer, 1920; Ehrenberg, 1928) *E. becraftensis* (Fig. 1.4D) are particularly scant. Clarke (1900) originally described his specimens from calcareous beds of the Oriskany as the casts of calyces, whereas Springer (1920) suggested, and Ehrenberg (1928) agreed, that only the "base" of these *E. becraftensis* specimens was preserved, meaning that they were not entire calyces. The RR could conceivably have been preserved, but it is most likely that specimens of *E. becraftensis* are internal molds (Clarke, 1900) of IB-B cones. The only previous worker to suggest which plates or plate circlets are represented as the internal molds was Ehrenberg (1928), who believed that at least the fused, proximally rounded BB were preserved. According to Clarke (1900), a single specimen shows "the upper edge of the calyx" (p. 62); otherwise, no specimen bears evidence of plates (Clarke, 1900) or an attached lifestyle (Ehrenberg, 1928). Notably, specimens definitively identified as *E. sacculus* are also reported from the same formation (Goldring, 1923); so, any spatial or temporal disparity between *E. sacculus* and *E. becraftensis* is absent. Clarke (1900), Springer (1920), and Ehrenberg (1928) described *E. becraftensis* as elongate, slender or narrow, and conical, much like the infillings that the ventral cavities of some *E. sacculus* would create (Fig. 1.4D). The range of representative measurements that Springer (1920) gave for *E. saccul*us accommodates some measurements he gave for the relatively large (Springer, 1920; Ehrenberg, 1928) *E. becraftensis,* and the internal mold of even a partial crinoid calyx may be smaller than the original calyx. Additional similarities were identified by Ehrenberg (1928), who noted that deposition of calcite, and therefore lengthening of the cup, continued after *E. sacculus* and *E. becraftensis* detached from a juvenile stem. Furthermore, he observed elongated specimens of *E. sacculus* remarkably similar to *E. becraftensis* and suggested that young *E. becraftensis* and young *E. sacculus* have nearly identical IB-B cones. Hence, we believe that *E. becraftensis* is probably a junior synonym of *E. sacculus.*

Twenty years after Clarke (1900), Springer (1920) designated an attached species, *E. holopoides*, from the Oriskany Sandstone of Maryland (Fig. 5.2C, G, I, Fig. 5.3H). Originally, Hall (1859) interpreted attached *Edriocrinus* as immature individuals, but attachment is not necessarily an indicator of immaturity among *Edriocrinus* species. As noted above, fusion of the IB-B circlets, not lifestyle or the shape of the base in adulthood, is associated with maturity. Regarding *E. holopoides*, Springer described it as a relatively large species, smaller and more compact than *E. sacculus* and sessile in adulthood (Springer, 1920; Ehrenberg, 1928). The shape of the wide, flat, encrusting base (Fig. 5.2C) reflected the shape of the attachment surface, although the base may be angled relative to its substrate (Springer, 1920; Ehrenberg, 1928). Like *E. sacculus,* no stem or evidence of a stem is present in adulthood (Springer, 1920; Ehrenberg, 1928). Both Springer (1920) and

Ehrenberg (1928) described slight differences between the cups, calyces, and crowns of *E. sacculus* and those of *E. holopoides*, and Springer primarily justified designation of the new species *E. holopoides* with the number of PBrBr (Springer, 1920). He studied 63 adult individuals collected from the same locality and counted the PBrBr of those with one or more preserved arms that did not enroll below PBr$_n$ax. He identified 42 unattached adults as *E. sacculus*, with 10 or more PBrBr. He also identified the remaining 21 attached adults as *E. holopoides*, with 5–7 PBrBr (Goldring, 1923), and therefore concluded that the number of primibrachs shown by a minority of the *Edriocrinus* collected could distinguish the two species. Other differences between *E. holopoides* and *E. sacculus* include the thinner walls; the wider, bowl-shaped ventral cavity; the straight-sided IB-B cone, as opposed to the angled sides of *E. sacculus*' IB-B cones; the shorter base; and the shorter arms of *E. holopoides.* However, these so-called differences simply reflect small variations in shape and size that are normal among representatives of any species of *Edriocrinus.* Also, no spatial or temporal disparity exists between *E. sacculus* and *E. holopoides.*

Several striking similarities between *E. holopoides* and *E. sacculus* are also included in Springer's (1920) original description. The IB-B cone widens upward toward the RR, and the sutures between the RR are visible (Ehrenberg, 1928). An identical large RA is in line with the RR, which are below the same wide (Ehrenberg, 1928), branching, nonpinnulate arms. The arms curve inward distally to varying degrees and bear the same prominent, V-shaped adoral groove. Overall, Springer (1920) observed the attached lifestyle and the other variations mentioned above, but as he also observed: "Calyx and arms otherwise similar to these of *E. sacculus*, except that the arms are shorter and their inrolled cluster relatively not so wide" (p. 452) (Fig. 5.2G, I). Other workers also found similarities between *E. holopoides* and *E. sacculus.* Broadly, Ehrenberg (1928) found evidence in both species of their calcite deposition continuing into maturity. The specimen Springer designated the holotype of *E. holopoides* had been previously identified as *E. sacculus* (Ohern, 1913; Goldring, 1923). More specifically, even partial specimens show similarities; for example, Ehrenberg (1928) found the IB-B cones of young *E. sacculus* and young *E. holopoides* difficult to distinguish. All of the measurements of *E. holopoides* are smaller than measurements of *E. sacculus* (Springer, 1920), but they all seem to fall within the lower size range of *E. sacculus*. Based on the small variations and significant similarities, *E. holopoides* is synonymized with *E. sacculus.*

Edriocrinus pyriformis Hall, 1862

Figures 5.4, 5.5

Holotype. —Cotypes, aboral cups (AMNH 37739–37741) from the Devonian Coeymans Formation, Eastman's Quarry, southeast of Utica, Oneida County, New York.

Diagnosis. —Fused IBB and BB form a short, flexed, stem-like peduncle for attachment; RR and RA high and narrow, forming a pear-shaped "false cup."

Description. —Dorsal cup medium to large, 30–40 mm high, 21 mm wide, with greatest width at level of mid-RR (Fig. 5.4B, 5.5B, C); IB-B cone has hollow stem-like form and is often irregularly curved, bent, or flexed before cementation to substrate (Fig. 5.4F, G, H, 5.5A, B, C). RR and RA compose majority of upper portion of cup (Fig. 5.4B, Fig. 5.5B, C), which is 19–25 mm high. R circlets expand outwardly and upwardly like the bottom of a vase and are commonly angled relative to IB-B cone (Fig. 5.4B, 5.5B, C). Five IBB tightly joined in a distinct circlet, with subtle, straight sutures, included at base of peduncle, which was cemented to substrate (Fig. 5.4A, F, G, I, Fig. 5.5A, B, C); lowermost portions of IB circlet irregular, broken, or with attachment scar (Fig. 5.4F, G, H, Fig. 5.5A) (Hall, 1862; Bather, 1900; Kirk, 1911; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Shimer and Shrock, 1944; Clement and Brett, 2015). Sutures between IBB and BB scalloped (Fig. 5.5B, C); five BB elongate, hexagonal to pentagonal in shape, semi-circular in transverse outline, together forming a flexed, cylindrical to conical shape that is the distal part of peduncle, up to 7 mm in diameter (Fig. 5.4I); sutures between BB straight to curved, following contour of peduncle (Fig. 5.4I). Sutures between BB and RR scalloped; proximal portions of R circlet oriented at angle to B circlet; five RR tumid, elongate, pentagonal, 19–25 mm high, 7–12 mm wide, sigmoidal in cross-section with greatest width at mid-plate, after which RR gently angle inward toward distal margin with R facets (Fig. 5.5B, C). Margins of RR crenulated (Fig. 5.5B). Pentagonal RA in line with RR, narrower than RR, very slightly projecting above level of RR, sutures in R circlet straight, following contour of the plate (Fig. 5.5B); R facets planate to slightly inward oriented, plenary, muscular, with prominent transverse ridge (Fig. 5.4D). Arms, tegmen, and anal sac unknown.

Remarks.— Like all *Edriocrinus* species, *E. pyriformis* lost a probable early stem at maturity, only to fabricate its IBB and BB into a thickened peduncle (Fig. 5.4B, Fig. 5.5 A, B, C) (Hall, 1862; Kirk, 1911; Jaekel, 1914; Wanner, 1915; Springer, 1920; Goldring, 1923, 1938; e.g., Ehrenberg, 1928), which was likely incapable of bending relative to a true crinoid stem. Unlike *E. pocilliformis* and *E. sacculus,* which may have been able to drag their cups, *E. pyriformis* remained attached and immobile, as previously described (Hall, 1862; Bather, 1900; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Clement and

Brett, 2015). No other *Edriocrinus* species approaches any kind of secondary stem development. The RR of this species are unusually high and narrow relative to all other *Edriocrinus* species (Fig. 5.5B, C).

Edriocrinus dispansus Kirk, 1911

Figure 5.6

1911 *Edriocrinus dispansus* Kirk, p. 112, pl. 11, figs. 1–2.

1919 *Edriocrinus adnascens* Dunbar, pl. 2, fig. 10 (*nomen nudum).*

1919 *Edriocrinus pyramidatus*; Dunbar, pl. 2, fig. 15 (*nomen nudum).*

1920 *Edriocrinus adnascens* Dunbar, p. 120–121, pl. II, fig. 3.

1920 *Edriocrinus adhaerens* Springer, p. 446, p. 451, pl. LXXVI, figs. 16–18.

1923 *Edriocrinus dispansus*; Goldring, p. 453–454, text fig. 62, pl. 58, figs. 19–21.

1928 *Edriocrinus dispansus*; Ehrenberg, pl. VI, figs. 7a–c.

1928 *Edriocrinus adhaerens*; Ehrenberg, pl. VI, fig. 6.

1944 *Edriocrinus dispansus*; Shimer and Shrock, p. 205, pl. 79, figs. 33a–b.

1963 *Edriocrinus dispansus*; Strimple, p. 17, p. 125–126, pl. 10, figs. 5–6.

1976 *Edriocrinus ata* Prokop, p. 188, pl. I, figs. 1–2.

1976 *Edriocrinus tara* Prokop, p. 188–189, pl. I, fig. 3, pl. II, figs. 1–2, pl. III, figs. 1–4.

1976 *Edriocrinus cylindricus* Prokop, p. 190, pl. IV, figs. 1–4.

1977 *Edriocrinus adnascens*; Strimple, p. 171, p. 173, figs. 1a–c.

1978 *Edriocrinus dispansus*; Strimple in Moore and Teichert, figs. 548,1b–c.

1987 *Edriocrinus ata* Prokop, p. 104–106.

1995a *Edriocrinus* cf. *ata*; Prokop and Petr, p. 105–106, pl. 1, figs. 1–2.

1995b *Edriocrinus ?ata*; Prokop and Petr, p. 49–50, pl. 1, figs. 1–3.

1995b *Edriocrinus ?tara*; Prokop and Petr, p. 49–50, pl. 1, figs. 4–16.

1997 *Edriocrinus* aff. *dispansus*; Le Menn, p. 136, figs. 2a–c.

2014 *Edriocrinus sp.*; Prokop and Turek, p. 219–220, pl. 1, figs. 1–4.

2015 *Edriocrinus adnascens*; Clement and Brett, p. 68–69, pl. 11, fig. 2, fig. 7.

2015 *Edriocrinus dispansus*; Clement and Brett, p. 69, pl. 11, fig. 3.

Holotype. —Aboral cup (USNM 27757) from the Devonian Birdsong Shale Member, Ross Formation, Big Sandy River, Benton County, Tennessee.

Diagnosis. —Laminated IB-B and dorsal cups, cones, and disks form a variety of disk to globose shapes for attachment. RR and RA, where known, strongly sloping inward, adorally, creating a truncated cone.

Description. —IB-B and dorsal cups, cones, or disks small to medium, low, discoid to bowl-shaped, or truncated-conical (like a squat Erlenmeyer flask) with flat, wide base of fused IB circlet, if present, and/or B circlet; plates in cup smooth and thick or thin (Fig. 5.6G, H). Inasmuch as R circlet is nearly always absent, mostly fused IB-B cups, cones, or disks are known (Fig. 5.6A, B, I, J, K). Fused IB-B cup, cone, or disk may be subglobose, globe-shaped, crateriform, tubular, or discoid (Fig. 5.6B, A, D, E, K, J) and was used for resting on the sediment or substrate attachment; IB-B cup, cone, or disk grows outwardly by addition of calcite laminae around entire cup, cone, or disk (Fig. 5.6B); IB-B cups, cones, or disks show external apices of BB visible from side, with tumid, vertical, or sloping sides bearing six, subtle, scalloped sutures, and internal scalloped sutures with intervening ridges for the reception of RR and RA (Fig. 5.6 A, B, F, J). Five RR and one RA high, proximally wide, tapering distally, typically forming most of visible dorsal cup; sutures in R circlet straight and depressed; R circlet conical and inward-sloping adorally with R facets forming a slightly elevated and indented cylindrical neck; facets planate, plenary, and muscular. RA in line with RR, not as wide, and not projecting above RR (Fig. 5.6G, H). Arms, tegmen, and anal sac unknown.

Remarks.—*E. dispansus* is characterized by a diversity of shapes of the dorsal or IB-B cup, cone, or disk and few other characters (Fig. 5.6A, B, C, D, E, F, G, H, K). However, despite the variety of cup, cone, or disk shapes, their consistently laminated nature (Fig. 5.6A, B, D, F, J) demonstrates that *E. dispansus* is an *Edriocrinus* species. *E. dispansus* frequently has the fewest visible, preserved plates of all *Edriocrinus* species, occasionally reduced to a rim of IB-B circlets merged into cups, cones, or disks on an encrusted surface (Fig. 5.6A, B, E). In fact, *E. adnascens* Dunbar, 1920, *E. adhaerens* Springer, 1920, *E. ata* Prokop, 1976, *E. tara* Prokop, 1976, and *E. cylindricus* Prokop, 1976 are only known from IB-B cups, cones, or disks, and only five known specimens of *E. dispansus* Kirk, 1911, have retained their RR and RA (Fig. 1.4I, Fig. 5.6A, B, E, G, H) (Kirk, 1911; Springer, 1920; Goldring, 1923; Shimer and Shrock, 1944; Ehrenberg, 1928; Le Maître, 1954, 1958a; Le Menn, 1997; Prokop and Turek, 2014; Clement and Brett, 2015). Therefore, the set of characteristics that they can be observed to share is unusually limited. Like other

Edriocrinus species, the IBB and BB are solidly fused and laminated, the apices of the tumid BB are visible in side view, the tumid BB create a lobate ventral cavity, and the R facets are planate, plenary, and muscular (Fig. 5.6A, B, D, E, G, H, J).

We assume that like all *Edriocrinus* species, the IBB and BB are fused into a shallow disk or cone. However, the IBB of many *E. dispansus* are particularly difficult to distinguish relative to the other species because of their largely attached nature (Fig. 1.4I, Fig, 5.6A, B, E) and have never been reported. Because *E. dispansus* specimens are much less complete than other *Edriocrinus* species and many are still embedded in their matrix, it is more challenging to explore the possibilities of ecophenotypic variation (Fig. 5.6A, B). Nonetheless, it is evident from the literature and the measurements given therein that individual researchers have described minor variations of cup, cone, or disk shape and size, which are normal among *Edriocrinus* species, as distinct species, which we have synonymized herein. Only the largest of the synonymized species, the original *E. dispansus* Kirk, 1911 seems to have rested on the sediment, whereas all others were permanently cemented in adulthood (Fig. 5.6A, B, H).

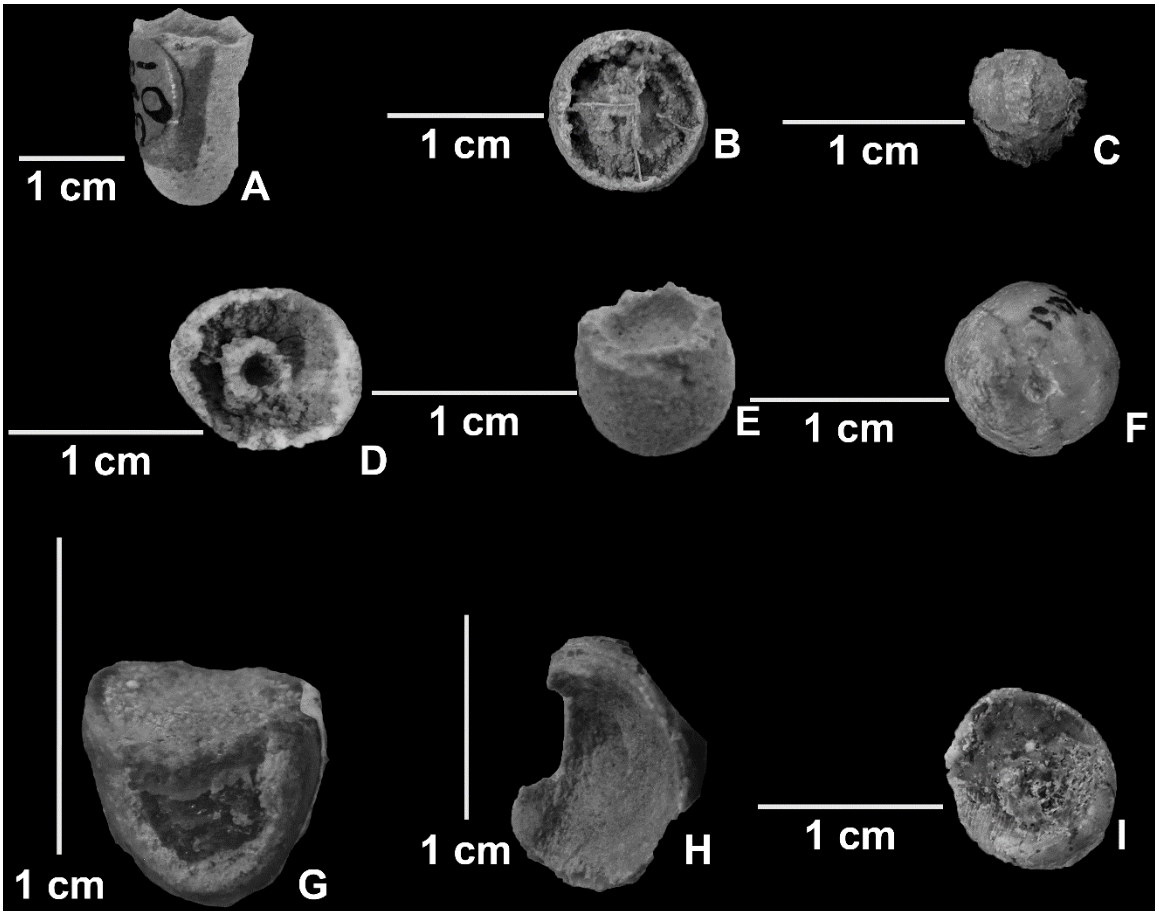

Figure 5.1 *E. pocilliformis*. A: Fused IBB and BB, USNM 97727. B: Four partitions, USNM 33993. C: Four partitions? USNM 1900. D: Inner IB shelf or stem fragment, USNM 1902. E: Infrabasal shelf, USNM 1902. F: Possible external stem, USNM 1900. G: BB weathering away from IBB, C2965. H: Faintly laminated IB-B cone, C2965. I: Inner IB shelf or stem fragment, USNM 1900.

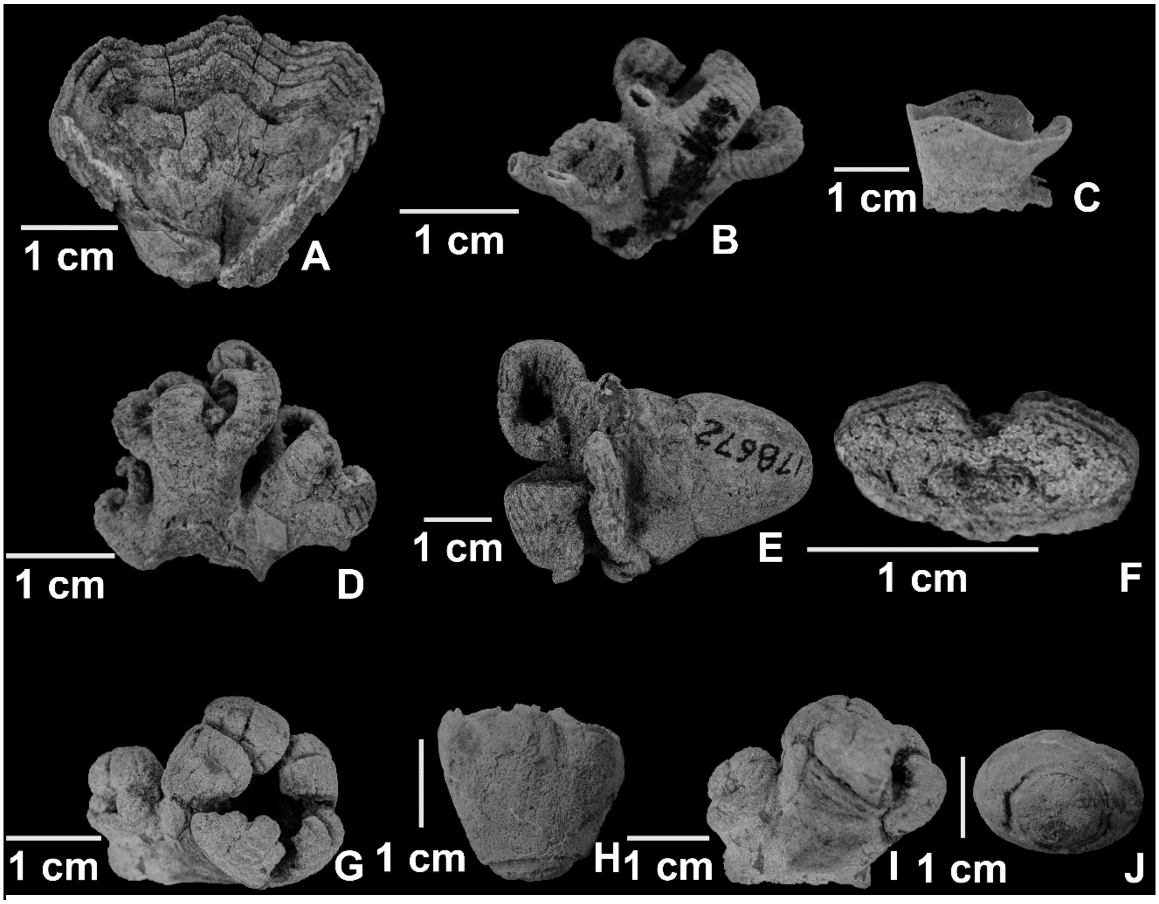

Figure 5.2 *E. sacculus*. A: Laminated, fused IB-B cone, USNM 1910. B: Curved arms; multiple attached individuals? USNM 57504. C: Encrusting IB-B cup, USNM 1901. D: Curved arms; multiple attached individuals? USNM 57504. E: Narrow RA within radial circlet, USNM 178672. F: Muscular articulation between BrBr, USNM 178672. G: Curved, branched arms, USNM 1901. H: Overgrowth of stem by IBB and overgrowth of IBB by BB, unnumbered Illinois specimen. I: Compact, attached form, USNM 1901. J: Overgrowth of stem by IBB and overgrowth of IBB by BB, unnumbered Illinois specimen.

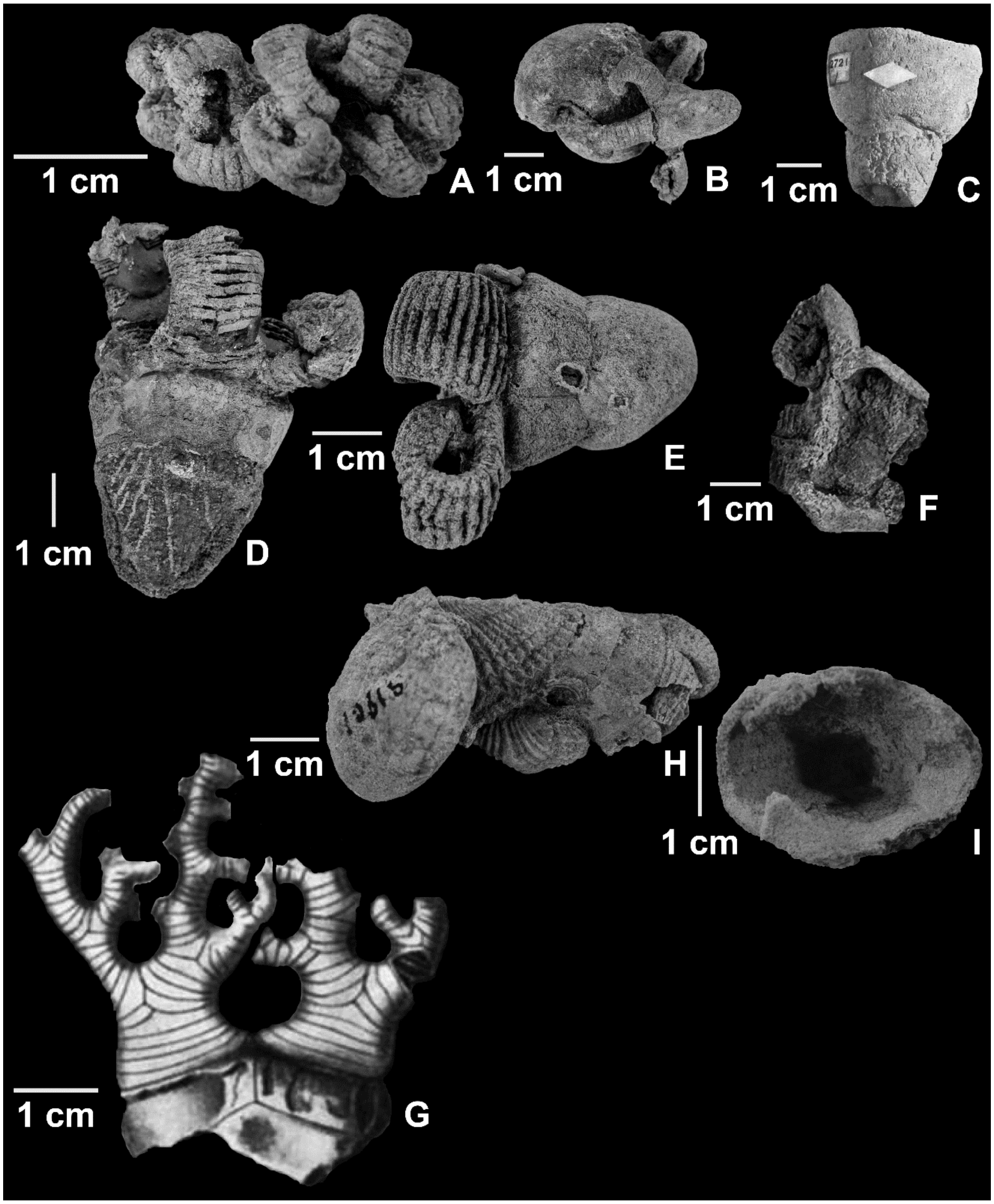

Figure 5.3 *E. sacculus*. A: Curved, branched arms, USNM 57504. B: PBrBr 4–17 axillary, USNM 57504. C: Overgrowth of stem by IBB and overgrowth of IBB by BB, modified from Ehrenberg, 1928. D: Two? anal plates, USNM 1910. E: Sutures depressed, USNM 178672. F: AmbAmb, Adambamb, USNM 1910. G: Arms proximally isotomous, distally heterotomous, composed of up to seven brachitaxes, modified from Wanner, 1915. H: Encrustation? of brachiopod, USNM 1901. I: Faintly striated IB-B cup, SUI 31507.

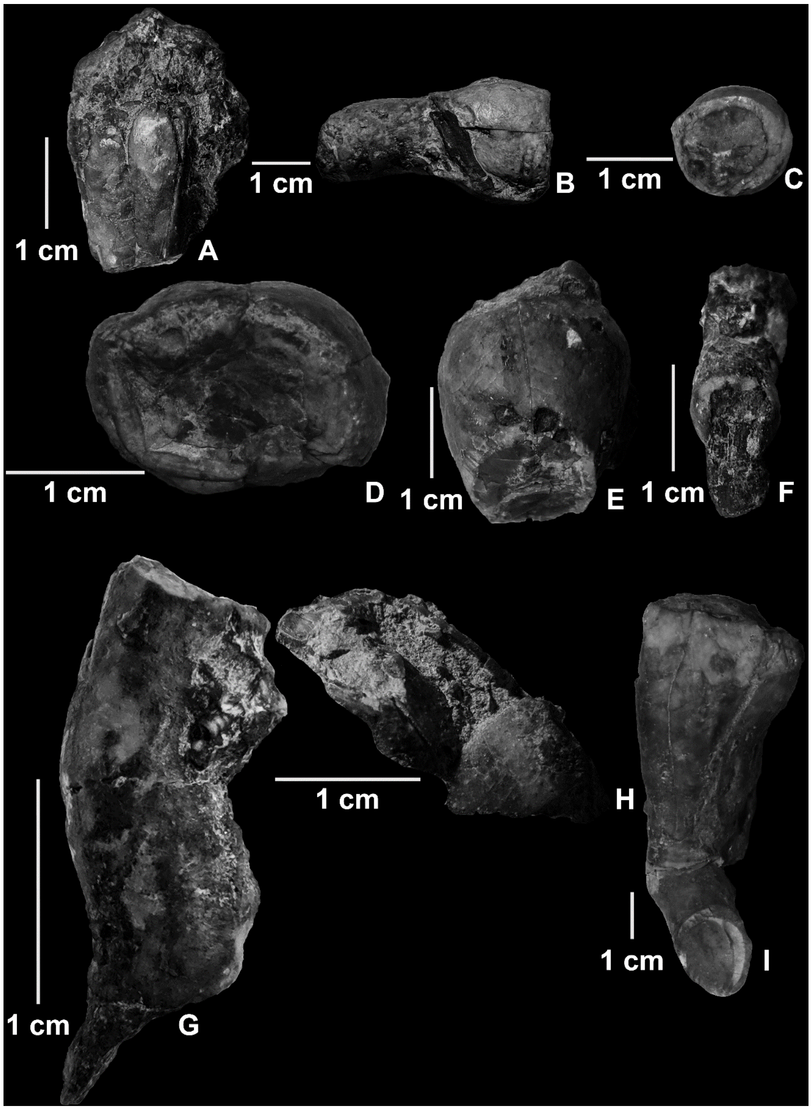

Figure 5.4 *E. pyriformis.* A: Thickened peduncle with subtle, straight sutures between five IBB, CMCIP 55739. B: R circlet composes majority of upper portion of cup, commonly angled relative to IBB and BB, CMCIP 37144. C: Attached lower portions of IBB, CMCIP 37144. D: Plenary, muscular radial facets, CMCIP 37144. E: Five IBB tightly joined with subtle, straight sutures, CMCIP 55739. F: Irregular lowermost parts of IBB, CMCIP 55739. G: Irregular lowermost parts of IBB, peduncle flexed, CMCIP 55739. H: Pustulose plates, CMCIP 37078. I: Five IBB tightly joined, subtle, straight sutures between elongate BB, CMCIP 55739.

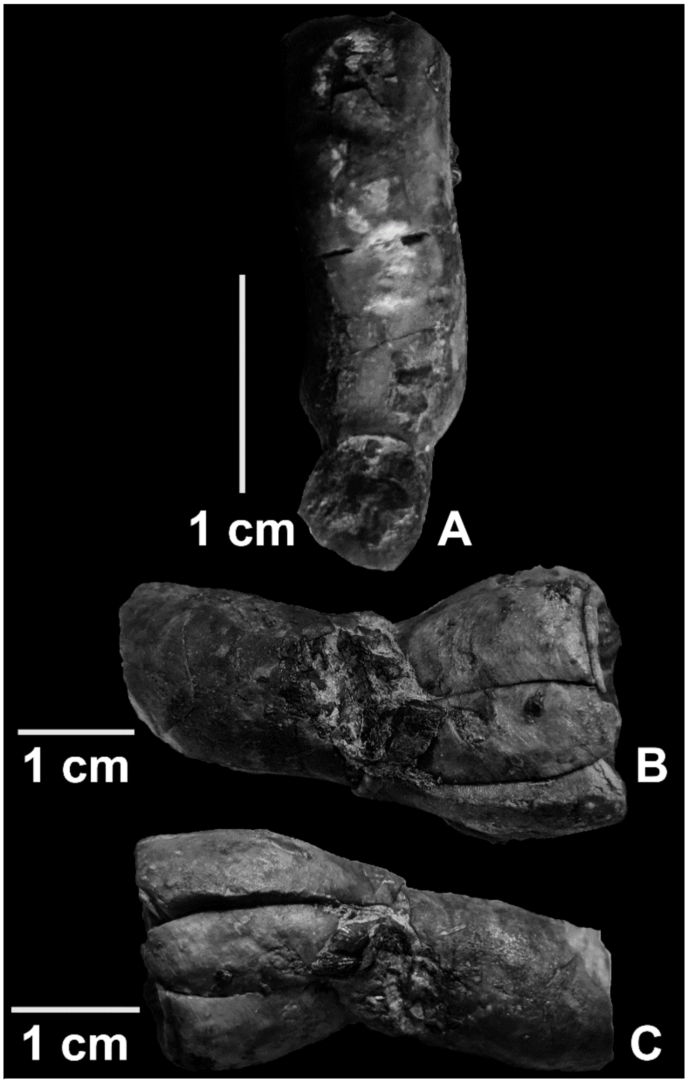

Figure 5.5 *E. pyriformis.* A: Peduncle bent or flexed, lowermost parts broken, suggesting substrate attachment, CMCIP 55739. B: Margins of RR crenulated, CMCIP 37144. C: R circlet high and narrow, CMCIP 37144.

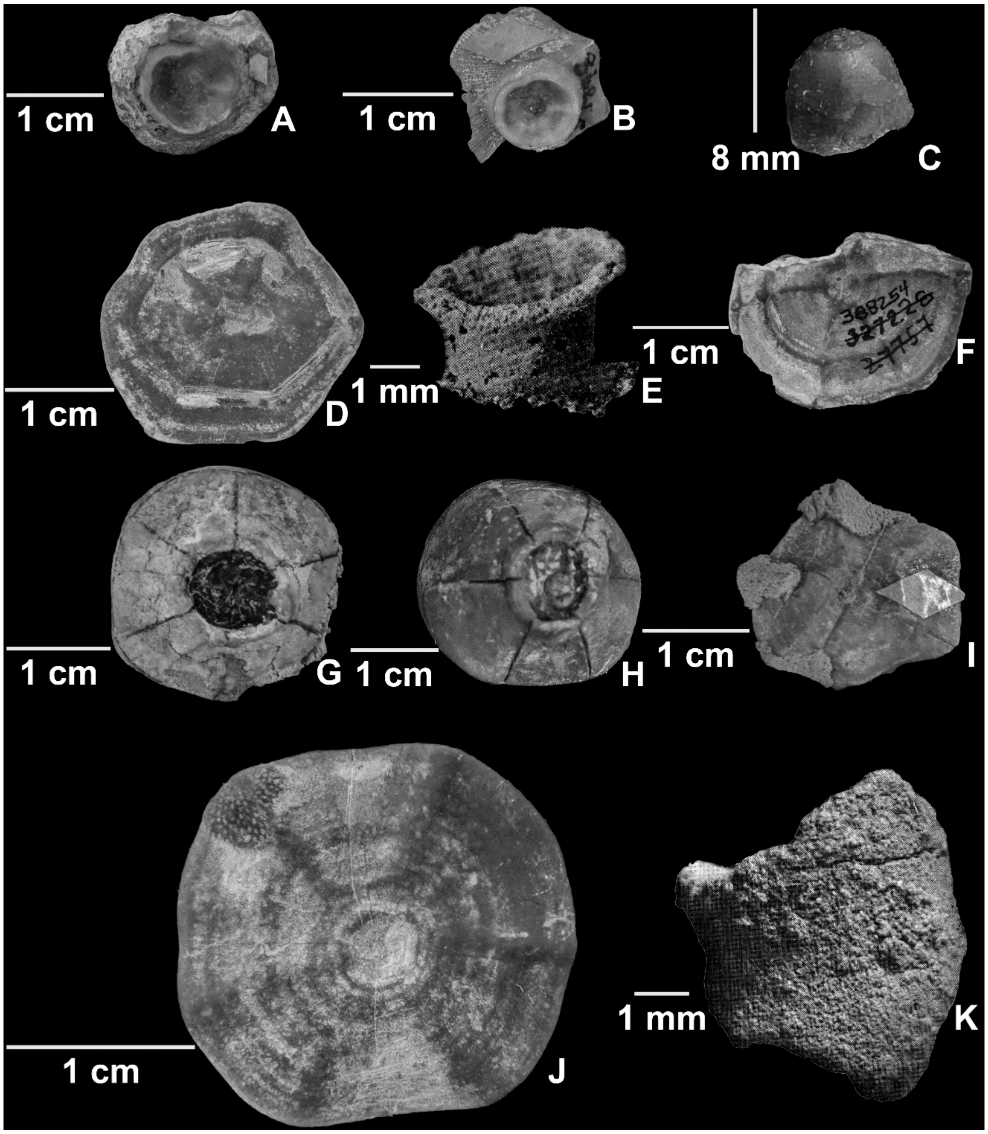

Figure 5.6 *E. dispansus.* A: Laminated IB-B circlets, USNM 1898. B: Attached, encrusting, laminated, partial specimen, USNM 1898. C: Possible arms, modified from Davis, no date. D: Crateriform IB-B circlets; scallops and ridges, USNM 327228. E: Tubular IB-B circlets with lobate ventral cavity, modified from Prokop, 1976. F: Scallops and ridges, USNM 327228. G: Radial circlet, USNM 1899. H: Radial circlet and plenary radial facets, USNM 27757. I: Fused, laminated IB-B circlets, USNM 1899. J: Laminated, discoid lower circlets, USNM 327228. K: Tubular IB-B circlets, modified from Prokop, 1976.

CHAPTER 6. DISCUSSION

6.1 Paleogeographic and paleoclimatic settings

Edriocrinus fossils are presently known from rocks deposited between the end of the Tippecanoe Sequence and the beginning of the Kaskaskia Sequence. *Edriocrinus* lived during a period of eustatic lowstand in early phases of the Acadian Orogeny (tectophases 1 and 2; Ettensohn, 1984). Occurrences of the crinoid (Fig. 1.1), ranging from isolated plates to complete individuals, are known from Laurussia (Laurentia, Avalonia, and Baltica) and northern Gondwana throughout present-day southern and eastern North America, southern England, northern Africa, and parts of central Europe. The genus is known from five countries, England, Algeria, Germany, the Czech Republic, and the United States, but the known occurrences were not widespread in any Early–Middle Devonian seas (Fig. 1.1). Most known specimens are from Laurussia, now the central and eastern USA, but this overrepresentation relative to the African and European specimens may reflect a taphonomic bias (e.g., Brett et al., 1997; Deline and Thomka, 2017) and/or a collection bias. Nevertheless, parts of Laurussia (the south-central to north-central USA), where *Edriocrinus* lived, were within the Eastern Americas biogeographic realm, namely the Appohimchi subprovince (e.g., Heckel and Witzke, 1979; Witzke et al., 1979; Boucot, 1985). *Edriocrinus* is considered endemic to eastern and central North America during the Lockhovian–Pragian, but by late Pragian time the genus was largely restricted to eastern North America (Witzke et al., 1979). Within the Old World realm, *Edriocrinus* occurred in Avalonia, Bohemia, and northern Gondwana, of the Rhenish-Bohemian region (Witzke et al., 1979; Boucot, 1985). Overall, *Edriocrinus* lived at ~25°–35° south latitude in the subtropical to warm-temperate climatic zone (Fig. 1.1). The Eastern Americas realm was probably not quite as warm as the Old World realm (Boucot, 1985; e.g., Scotese and McKerrow in McKerrow and Scotese, 1990). Regarding paleocurrents, the Eastern Americas realm primarily bordered a counterclockwise, cool subtropical gyre, whereas the Rhenish-Bohemian region of the Old World realm was characterized by a counterclockwise, warm subtropical gyre (Heckel and Witzke, 1979). Storms were also common within this zone (Marsaglia and Klein, 1983), and such a pattern may have facilitated larval dispersal throughout the Rheic Ocean (Fig. 1.1).

However, by Middle Devonian (early Eifelian) time when *Edriocrinus* apparently went extinct, the genus range had become limited to the Bohemian microplate and possibly northeastern North America. Early Eifelian-age European carbonates from the Czech Republic include siliciclastics and black shales, likely related to global tectonic and eustatic events that contributed to anoxia during the Chotec Event (Chlupác, 1988; Hladil, 1988; Copper, 2002). In North America, a change from limestones to dark, calcareous shales represents eustatic sea-level rise and resulting deepening and hypoxia associated with the slightly younger Bakoven Event (DeSantis and Brett, 2011). Thus, the changing sea levels and oxygen levels during the Chotec and Bakoven Events may have been factors in the extinction of *Edriocrinus*.

6.2 Depositional environments and life modes

As shown by the variety of lithologies in which *Edriocrinus* occurs (Table 6.1, Table 6.2, Fig. 6.3), *Edriocrinus'* phenotypic plasticity evidently gave it the flexibility to live in many different environments. As a genus, no single preferred set of environmental conditions emerges from the lithologies in Table 6.1 during any part of its geologic range.

Furthermore, given that some *E. dispansus* were epiplanktic (e.g., Schuchert, 1906; Kirk, 1911; Springer, 1920; Ehrenberg, 1928; Strimple, 1977; Prokop and Petr, 1995a; Frest et al., 1999; Prokop and Turek, 2014; Clement and Brett, 2015), encrusting the hard surfaces of living, floating hosts to remain in the water column throughout their lives, a true relationship may not exist between the depositional setting and the preferred environments of encrusting, pelagic *E. dispansus* (Fig. 6.3). In any case, most *Edriocrinus* species *(E. pocilliformis, E. pyriformis*, and *E. dispansus*) appear in the fossil record shortly after the inception of Early Devonian (Lockhovian; Helderbergian) time at ~419 Ma (Becker et al. in Gradstein et al., 2020).

E. pocilliformis appears to have been restricted to Lockhovian (Helderbergian; Swezey, 2002) time, occurring throughout east-central United States (Table 6.1 and references therein). One unit that ranges in age from Lockhovian–Emsian (Helderbergian–?Deerparkian; has yielded specimens identified herein as *E. pocilliformis*, as well as possible *E. pocilliformis* specimens. During the brief existence of *E. pocilliformis* (~7.6 m.y.; Becker et al. in Gradstein et al., 2020), (Fig. 6.2), its unattached, epifaunal or semi-infaunal lifestyle enabled life in both high- and low-energy settings (Fig. 6.3) based on its lithologic occurrences (Table 6.1; e.g., Dunbar, 1919; Wilson, 1949; Cleaves et al., 1968; Rickard, 1975; Broadhead et al., 1988; Smosna, 1988; Epstein, 1989; Monteverde, 1992; Harrison, 1999). Similarly, probable *E. pocilliformis* specimens from the Bailey Limestone of Missouri (Tansey in Branson, 1922) likely lived in a lower-energy setting as suggested by their occurrence in argillaceous, fine-grained limestones (Table 6.1; e.g., Harrison, 1999). Mobility may have been part of its unattached lifestyle, based on the model of

Agassizocrinus (Ettensohn, 1975), using its arms to move as suggested herein for *E. sacculus*.

Most of the attached and unattached forms of *E. sacculus,* including probable forms from Maine, (Table 6.1 and references therein) occur in high-energy, nearshore, sandy settings (Table 6.1; e.g., Kayser, 1885; Schlüter, 1900; Jaekel, 1914; Wanner, 1915; Cloos, 1951; Rickard, 1975; Diecchio et al., 1984; Drake et al., 1996; Nelson, 1998; Hollick, Shail, and Leveridge, 2006; Leveridge, 2011), but a few are known from lower-energy, silty settings (Fig. 6.3) (e.g., Boucot, 1961, Hall, 1970; Kite and Kammer, 1988; Harper, 1999; Hollick, Shail, and Leveridge, 2006; Leveridge, 2011). Attached forms of *E. sacculus* demonstrate an encrusting, epifaunal life mode, whereas many unattached individuals apparently inserted their cups into mobile sands, assuming a vagile, semi-infaunal life mode like that of *Agassizocrinus* (Ettensohn, 1975). *E. sacculus* lived during Pragian–Emsian (late Helderbergian–Esopusian) time (~12.4 m. y.; Becker et al. in Gradstein et al., 2020) (e.g., Carlson et al., 1987; Boucot and Wilson, 1994; Swezey, 2002; Wehrmann et al., 2005; Leveridge, 2011) occurring in the eastern and central United States, Germany, and southern England in Cornwall (Fig. 6.2, Table 6.1 and references therein). From a single specimen (Fig. 5.3B), Kirk (1911) interpreted this species as having been able to crawl "upside-down," carrying its cup above the arms. The specimen is preserved with distal ends of the arms in contact with a gastropod shell but provides no indication of original orientation. The remains of these two animals were fortuitously buried in contact, creating an oddity of preservation and the illusion that *Edriocrinus* could move “upside-down.” Although some modern crinoids crawl oral-side up, no evidence exists to support the possibility of crinoids crawling oral-side down.

E. pyriformis first appeared in Eifelian (Southwoodian; Rickard, 1975; Swezey, 2002) time (e.g., Hall, 1862; Goldring, 1923, 1938; Bassler and Moodey, 1943; Rickard and Zenger, 1964; Brett and ver Straeten, 1994; Clement and Broadhead, 1994; Clement and Brett, 2015). Some workers have suggested that purported *E. pyriformis* specimens range from Lockhovian to Eifelian (Helderbergian–Southwoodian) (Fig. 6.2) time (Clement and Brett, 2015). Nevertheless, *E. pyriformis* specimens were probably attached with a "false stem" derived from the elongated IB and B circlets of the cup and occurred in muddy carbonates (Fig. 6.3) (e.g., Wilson, 1949; Laporte, 1969; Rickard, 1975; Broadhead et al., 1988; Brett and ver Straeten, 1994), suggesting a semi-infaunal life mode. The species is known from eastern and central United States (Table 6.1 and references therein).

E. dispansus was the longest-lived *Edriocrinus* species (Fig. 6.2), persisting from Lockhovian through Eifelian (Helderbergian–Southwoodian; e.g., Prokop and Petr, 1995a; Boumendjel et al., 1997a; Le Menn, 1997; Paris et al., 1997; Plusquellec et al., 1997; Swezey, 2002; Parsley and Sumrall, 2007; Prokop, 2013; Prokop and Turek, 2014) time and occurring in Algeria and throughout the Czech Republic and central United States (Table 6.1 and references therein). It was an epifaunal form that lived attached to hard substrates or utilized its broad cup to rest on more muddy substrates (e.g., Ettensohn, 1984). *E. dispansus* and probable *E. dispansus* specimens are known from both low- and high-energy settings (Dunbar, 1919; Wilson, 1949; Amsden, 1957; Broadhead et al., 1988; Prokop and Petr, 1995b; e.g., Velebilová and Šarf, 1996; Boumendjel et al., 1997a, b; Chlupáč, 2003; Mehadji et al., 2004; Koptíková et al., 2010; Koptíková, 2011; Prokop, 2013; Prokop and Turek, 2014; Bábek et al., 2018; Limam et al., 2021). In low-energy settings, they rested atop soft carbonate and clastic mud substrates, whereas those preserved in high-energy settings may have been transported (e.g., Clement and Brett, 2015). Some specimens from the Czech Republic occur in rocks interpreted as ancient slumps and calci-turbidites (Chlupáč, 1988; Chlupáč and Kukal, 1988; Buggisch and Mann, 2004; Bábek et al., 2018; Slavík and Hladil, 2020) and have almost certainly been transported. Attached forms may have lived on the hard parts of a variety of hosts in low-energy settings or on hosts similarly transported into high-energy settings (e.g., Clement and Brett, 2015). Attached *E. dispansus* encrusted the hard surfaces of other organisms, including the loboliths of *Scyphocrinites*, cephalopods, bivalves, brachiopods, pluricolumnals of other crinoids, holdfasts of other crinoids, gastropods, and hyoliths (Schuchert, 1906; Kirk, 1911; Dunbar, 1919, 1920; Springer, 1920; Ehrenberg, 1928; Amsden, 1958; Prokop, 1976; Strimple, 1977; Clement and Broadhead, 1994; Prokop and Petr, 1995a, b; Frest et al., 1999; Parsley and Sumrall, 2007; Prokop and Turek, 2014; Clement and Brett, 2015). Whether any of these hosts were alive or dead at the time of attachment is unresolved (Prokop, 1976; Prokop and Petr, 1995a; Prokop and Turek, 2014). Attached, epiplanktic *E. dispansus* may have "hitchhiked" on living, floating hosts such as cephalopods and the loboliths of *Scyphocrinites*. In contrast, attachment to any stationary host, living or dead, such as brachiopods or stemmed crinoids (e.g., Prokop and Turek, 2014) suggests a stationary lifestyle. Some *E. dispansus* and probable *E. dispansus* specimens occur only as individual calyx plates from a variety of environmental settings (Fig. 6.3) (Prokop and Petr, 1995b, Prokop and Turek, 2014), rendering their lifestyles difficult to determine.

Overall, the preservation of whole *Edriocrinus* calyces and crowns is exceptionally rare, with most of the specimens represented solely by the resistant infrabasal/basal cups, cones, and disks. As most *Edriocrinus* species are thought to have lived in shallow, agitated environments, wave agitation and storms likely were quick to disarticulate and rework the weaker, upper parts of the calyces and crowns.

6.3 Ecophenotypes among *Edriocrinus* species

Edriocrinus is a unique crinoid with unusual adaptations. For example, its stemlessness during the Paleozoic; use of the infrabasal-basal cone as a "stem;" the lamination and encapsulation of infrabasals by basals; and the large, raptorial arms with robust brachials are all features known individually in other crinoids. However, *Edriocrinus* stands alone as a genus in which all these aspects are combined. Naturally, the uncommon morphology of *Edriocrinus* has masked its phylogeny and the true nature of its features, some of which are not shared among any other crinoids. The uncertainty in phylogeny has only been further confounded by long-standing inappropriate classification. Indeed, specimens of *Edriocrinus* have not even been classified persistently as crinoids. Although it is certainly a crinoid, its placement within the Class Crinoidea has been uncertain since the genus was initially described by Hall (in Silliman et al., 1858).

Fourteen species of *Edriocrinus* (Fig. 1.4) have been recognized previously, but close, renewed examination of these species, aligned with a current understanding of speciation, suggests that the genus has been excessively split into species. Many of its previously defined species occur together, even in the same exposure. All previous *Edriocrinus* species were designated before the possibility of phenotypic plasticity was well established. Therefore, several *Edriocrinus* species were insufficiently justified by intraspecific variations developed for different environmental conditions because the variations were interpreted as taxobases.

As previously noted, the IB-B cup, cone, or disk of *Edriocrinus* is often the only preserved part of the crinoid, and many species were designated based only on the diverse shapes of the cups, cones, and disks. In fact, as has been shown in several other stemless crinoid genera and species (Ettensohn, 1975, 1980, 1981, 1984), a single species may have different cone shapes corresponding to adaptations for distinct environmental settings. Moreover, as the cup, cone, or disk of *Edriocrinus* is the part of the crinoid most in contact with a possibly dynamic substrate, it is also the most likely to show an assortment of adaptations corresponding to the degree of substrate stability. Naturally, the phenotypic expression of the cone will vary according to environmental conditions, creating ecophenotypes. Considering the likelihood of ecophenotypic variation, all of the 14 designated species have now been synonymized with only four well-defined species, *E. pocilliformis, E. sacculus, E. pyriformis,* and *E. dispansus* (Chapter 5). Of these species, *E. pyriformis* was the only one without apparent ecophenotypes; so, no junior synonyms are interpreted herein. On the other hand, the species *E. pocilliformis, E. sacculus,* and *E. dispansus* apparently developed ecophenotypes, which some previous workers (Springer, 1920; Goldring, 1923; Ehrenberg, 1928; e.g., Bassler and Moodey, 1943; Prokop, 1976; Frest et al., 1999; Clement and Brett, 2015) recognized as distinct species.

E. pocilliformis shows four dominant ecophenotypes, the most of any *Edriocrinus* species: distally flattened (Fig. 6.1A), distally rounded (Fig. 6.1B), distally tapered and rounded (Fig. 6.1D), or distally rounded with a flared collar (Fig. 6.1C). These shapes are similar to those of all species within the crinoid genus *Paragassizocrinus* and may occur in high-cone and low-cone variants (Ettensohn, 1980). In lower-energy environments with softer, fine-grained substrates, *E. pocilliformis* may have achieved stability through a ballasted (heavily calcified) cone or cup, including a distally flattened cup (epifaunal) or a distally tapered and rounded cone (semi-infaunal). The flared collar on some forms may have provided additional support as a prop in muddy settings where the cup was partially buried to the level of the collar.

E. sacculus shows two ecophenotypes with thick cups and robust arms, an unattached, semi-infaunal form and an attached, epifaunal form. Both forms are known from high-energy siliciclastic or calcarenitic environments (e.g., Hall, 1859; Kayser, 1885; Schlüter, 1900; Kirk, 1911; Ohern, 1913; Jaekel, 1914; Wanner, 1915; Springer, 1920; Ehrenberg, 1928; Cloos, 1951; Rickard, 1975; Diecchio et al., 1984; Drake et al., 1996; Nelson, 1998; Hollick, Shail, and Leveridge, 2006; Ettensohn, 2008; Leveridge, 2011). Therefore, the nature of the cup and arms may have been an evolutionary response to the shallow, high-energy, middle and lower shoreface environments of *E. sacculus* (e.g., Ettensohn, 1975, 1984). The large, ballasted cup of the unattached ecophenotype may be distally tapered. Such a morphology may have enabled insertion into loose, mobile sands and allowed some rocking movement within the sand, which was necessary to maintain stability and withstand highly agitated water, like the crinoids *Agassizocrinus* and *Paragassizocrinus* (Ettensohn, 1975, 1980). Distal abrasion of the cup may reflect high-energy conditions in shifting sands. The arms may have provided mobility or support, and if the brachials were angled or stepped in life, as they have been preserved, they may have been capable of lateral motions. The attached ecophenotype has a squared, more compact cup and shorter arms, and the crouching posture of these attached crowns, locally found in clusters, may have been an adaptation to very high-energy conditions.

The most variable *Edriocrinus* species is the epifaunal *E. dispansus,* with its diverse infrabasal-basal cup, cone, and disk shapes. It is also the most difficult to interpret because its infrabasals are often completely concealed by growth-related encapsulation or by attachment to a hard substrate. The typical, broad, flat base of the cup is the product of substrate encrustation or unattached, resting forms living on soft substrates, similar to the distally flattened, low-cone *E. pocilliformis* ecophenotype. The inward-sloping, narrowed nature of some preserved circlets may represent a more streamlined cup and arms for epiplanktic life.

Although *Edriocrinus* does share some of the above traits with other crinoids, such characters have likely arisen through convergent evolution. No doubt, many *Edriocrinus* characters have been misapplied when designating the genus and its species. Evidently, morphology of the cup was a dynamic, ecophenotypic trait.

Table 6.1 Occurrences of *Edriocrinus* from the literature

Unit	Location	Lithology	Stage	Relevant references
E. pocilliformis				
Corriganville Limestone, Helderberg Group	Washington County, Maryland, USA	calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Miller, 1889; Stose and Swartz, 1912; Amsden, 1951
Corriganville Limestone, Helderberg Group	southeast slope of Bull Pasture Mountain, 12.87 km (8 miles) southwest of Monterey, US Route 250, Highland County, Virginia, USA	calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Miller, 1889; Butts, 1940
New Scotland Limestone, Helderberg Group	Saugerties, Ulster County, New York, USA	calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Miller, 1889; Goldring, 1931; Chadwick, 1944
New Scotland Limestone, Helderberg Group	Helderberg Mountains, Clarksville, Albany County, New York, USA	calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Hall, 1859; Wachsmuth and Springer, 1885, 1886; Miller, 1889; Talbot, 1905; Springer, 1920; Goldring, 1923, 1931; Ehrenberg, 1928; Bassler and Moodey, 1943

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Corriganville Limestone, Helderberg Group	Panther Gap, Rockbridge County, Virginia, USA. Springer (1920) further stated that the specimens were collected near Covington, but Covington is in Alleghany County, Virginia, USA.	calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Miller, 1889; Springer, 1920; Ehrenberg, 1928; Bassler and Moodey, 1943
Bailey Limestone	Bailey's Landing, Perry County, Missouri, USA. Although Bailey's Landing no longer exists, this site is now in Salem Township, Perry County, Missouri.	shaly calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Meek and Worthen, 1868; Wachsmuth and Springer, 1885, 1886; Miller, 1889; Keyes, 1894; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Bassler and Moodey, 1943
Corriganville Limestone, Helderberg Group	Cumberland, Allegany County, Maryland, USA	calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Miller, 1889; Stose and Swartz, 1912; Ohern, 1913; Bassler and Moodey, 1943
Corriganville Limestone, Helderberg Group	Cherry Run, Morgan County, West Virginia, USA	calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Miller, 1889; Stose and Swartz, 1912; Ohern, 1913; Bassler and Moodey, 1943
New Scotland Limestone, Helderberg Group	Helderberg Mountains near Schoharie, Schoharie County, New York, USA	calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Miller, 1889; Goldring, 1923, 1931; Bassler and Moodey, 1943

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Birdsong Shale Member?, Ross Formation	Decatur County, Tennessee, USA	clay-shale, calcareous shale, minor calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	e.g., Miller, 1889; Dunbar, 1919; Springer, 1920; Goldring, 1923; Bassler and Moodey, 1943; Clement and Brett, 2015
Licking Creek Limestone, Helderberg Group	Bells Valley, Rockbridge County, Virginia, USA	calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	Swartz, 1929a, b
Licking Creek Limestone, Helderberg Group	Prices Bluff, 1.6 km (1 mile) north of Gala, Botetourt County, Virginia, USA	calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	Swartz, 1929a, b; Bassler and Moodey, 1943
Licking Creek Limestone, Helderberg Group	near Clifton Forge, Alleghany County, Virginia, USA	calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	e.g., Springer, 1920; Swartz, 1929a, b
Rockhouse Limestone Member?, Ross Formation	Linden, Perry County, Tennessee, USA	calcarenite interbedded with shale	Lockhovian (Helderbergian)	e.g., Miller, 1889; Dunbar, 1919; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Bassler and Moodey, 1943; Clement and Brett, 2015
Rockhouse Shale Member, Ross Formation	8.04 km (5 miles) southeast of Savannah, Hardin County, Tennessee, USA	calcisiltite, calcareous shale	Lockhovian (Helderbergian)	e.g., Miller, 1889; Dunbar, 1919; Goldring, 1923; Bassler and Moodey, 1943; Wilson, 1949
Corriganville Limestone, Helderberg Group	western Frederick County, Virginia, USA	calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Miller, 1889; Goldring, 1923; Butts and Edmundson, 1966

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
New Scotland Formation, Helderberg Group	near Stroudsburg and Delaware Water Gap, Monroe County, Pennsylvania, USA	silty shale; shaly calcisiltite and calcilutite; calcareous, siliceous, laminated shale	Lockhovian (Helderbergian)	e.g., Miller, 1889; Swartz, 1929a, b
Corriganville Limestone, Helderberg Group	21st Bridge northeast of Keyser, Mineral County, West Virginia, USA	calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Miller, 1889; Ohern, 1913; Swartz, 1913; Swartz et al., 1913
Licking Creek Limestone, Helderberg Group	Ernstville, Washington County, Maryland, USA	calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	Stose and Swartz, 1912; Swartz, 1913; Swartz et al., 1913
Licking Creek Limestone, Helderberg Group	North Mountain, Berkeley County, West Virginia, USA	calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	Stose and Swartz, 1912; Swartz, 1913; Swartz et al., 1913
Minisink Limestone, Helderberg Group	abandoned Nearpass Quarry 2.9 km (1.8 miles) southwest of Duttonville, Port Jervis South 7.5' Quadrangle, Sussex County, New Jersey, USA	shaly calcisiltite and calcilutite	Lockhovian (Helderbergian)	Swartz, 1929a, b
Ross Limestone Member, Ross Formation	Grandview, Bath Springs 7.5' Quadrangle, Hardin County, Tennessee, USA. This site is 12.87 km (8 miles) west of Clifton, Wayne County, Tennessee.	shaly calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Miller, 1889; Dunbar, 1919; Goldring, 1923; Bassler and Moodey, 1943; Wilson, 1949
E. pocilliformis?				

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Bailey Limestone	Little Saline Creek area of Sainte Genevieve County, Missouri, USA	shaly calcisiltite and calcilutite	Lockhovian (Helderbergian)	Tansey *in* Branson, 1922; Bassler and Moodey, 1943
Edriocrinus cf. pyriformis				
lower Rockhouse Limestone Member, Ross Formation	northern road cut on Tennessee Route 69, Decatur County, Tennessee, USA (35° 46'30" N 88° 05'0" W)	calcarenite interbedded with shale	Lockhovian (Helderbergian)	e.g., Clement and Broadhead, 1994; Clement and Brett, 2015
E. dispansus				
Haragan Formation, Hunton Group	south of Fittstown, Pontotoc County, Oklahoma, USA (NW 1/4 sec. 12, T. 1 N., R. 7 E.)	shaly calcisiltite and calcilutite	Lockhovian (Helderbergian)	Strimple, 1977
Birdsong Shale Member, Ross Formation	Big Lick Creek, Decatur County, Tennessee, USA	clay-shale, calcareous shale, minor calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	Dunbar, 1920; e.g., Ehrenberg, 1928; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Wilson, 1949; Strimple *in* Moore and Teichert, 1978; Frest et al., 1999; Clement and Brett, 2015

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Birdsong Shale Member, Ross Formation	Birdsong Creek, Benton County, Tennessee, USA	clay-shale, calcareous shale, minor calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	Dunbar, 1920; e.g., Ehrenberg, 1928; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Wilson, 1949; Strimple *in* Moore and Teichert, 1978; Frest et al., 1999; Clement and Brett, 2015
Birdsong Shale Member, Ross Formation	Perryville, Decatur County, Tennessee, USA	clay-shale, calcareous shale, minor calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	Dunbar, 1920; e.g., Ehrenberg, 1928; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Wilson, 1949; Strimple *in* Moore and Teichert, 1978; Frest et al., 1999; Clement and Brett, 2015
Haragan Formation, Hunton Group	west of Clarita, Coal County, Oklahoma, USA (near old Hunton townsite, sec. 8, T. 1 S., R. 8 E.)	shaly calcisiltite and calcilutite	Lockhovian (Helderbergian)	Strimple, 1963; e.g., Frest et al., 1999
Haragan Formation, Hunton Group	3.54 km (2.2 miles) south, 0.8 km (0.5 miles) east of Fittstown, Pontotoc County, Oklahoma, USA	shaly calcisiltite and calcilutite	Lockhovian (Helderbergian)	Strimple, 1963

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Ross Limestone Member, Ross Formation	8.04 km (5 miles) southeast of Savannah, Hardin County, Tennessee, USA	shaly calcisiltite and calcilutite	Lockhovian (Helderbergian)	e.g., Springer, 1920; Ehrenberg, 1928; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Strimple *in* Moore and Teichert, 1978
Birdsong Shale Member, Ross Formation	Steel bridge, Henry County, Tennessee, USA. This site is now ~8.7 km south of the US 79 bridge crossing the Tennessee River, likely underwater because the Tennessee Valley Authority has since created Kentucky Lake.	clay-shale, calcareous shale, minor calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	Dunbar, 1919; Bassler and Moodey, 1943; e.g., Shimer and Shrock, 1944; Wilson, 1949; Strimple *in* Moore and Teichert, 1978
lower Rockhouse Limestone Member, Ross Formation	Allens Mill, northern side of Birdsong Creek, Benton County, Tennessee, USA (35º55'45" N 88º05'15" W)	calcarenite interbedded with shale	Lockhovian (Helderbergian)	e.g., Kirk, 1911; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Strimple *in* Moore and Teichert, 1978; Frest et al., 1999; Clement and Brett, 2015

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
upper Rockhouse Limestone/lower most Birdsong Shale Members, Ross Formation (site exposes 5.1 m of Rockhouse Limestone and 13.2 m of Birdsong Shale)	Parsons Quarry, Tennessee Route 69, Decatur County, Tennessee, USA (35º41'15"N 88º06'15"W)	Birdsong Shale: clay-shale, calcareous shale, minor calcarenite, calcisiltite, and calcilutite. Rockhouse Limestone: calcarenite interbedded with shale.	Lockhovian (Helderbergian)	e.g., Bassler and Moodey, 1943; Shimer and Shrock, 1944; Strimple *in* Moore and Teichert, 1978; Clement and Brett, 2015
upper Rockhouse Limestone/lower most Birdsong Shale Members, Ross Formation (site exposes 3 m of Rockhouse Limestone and 2 m of Birdsong Shale)	road cut on Tennessee Route 69, Decatur County, Tennessee, USA (35º46'30"N 88º05'00"W)	Birdsong Shale: clay-shale, calcareous shale, minor calcarenite, calcisiltite, and calcilutite. Rockhouse Limestone: calcarenite interbedded with shale.	Lockhovian (Helderbergian)	e.g., Bassler and Moodey, 1943; Shimer and Shrock, 1944; Strimple *in* Moore and Teichert, 1978; Clement and Brett, 2015
upper Rockhouse Limestone/lower most Birdsong Shale Members, Ross Formation (site exposes 4.1 m of Rockhouse Limestone and 16.3 m of Birdsong Shale)	Benton Quarry, Tennessee Route 192, Holladay, Benton County, Tennessee, USA (35º52'30"N 88º07'15"W)	Birdsong Shale: clay-shale, calcareous shale, minor calcarenite, calcisiltite, and calcilutite. Rockhouse Limestone: calcarenite interbedded with shale.	Lockhovian (Helderbergian)	e.g., Bassler and Moodey, 1943; Shimer and Shrock, 1944; Strimple *in* Moore and Teichert, 1978; Clement and Brett, 2015

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Birdsong Shale Member, Ross Formation	7.24 km (4.5 miles) north of Holladay, Benton County, Tennessee, USA	clay-shale, calcareous shale, minor calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	e.g., Kirk, 1911; Dunbar, 1919; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Wilson, 1949; Strimple *in* Moore and Teichert, 1978; Clement and Brett, 2015
Birdsong Shale Member, Ross Formation	0.8 km (0.5 miles) east of Holladay, Benton County, Tennessee, USA	clay-shale, calcareous shale, minor calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	e.g., Kirk, 1911; Dunbar, 1919; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Wilson, 1949; Strimple *in* Moore and Teichert, 1978; Clement and Brett, 2015

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Birdsong Shale Member, Ross Formation	Swayne's Mill, 1.6 km (1 mile) upstream from the steel bridge, Henry County, Tennessee, USA. This site is now ~8.7 km south of the US 79 bridge crossing the Tennessee River, likely underwater because the Tennessee Valley Authority has since created Kentucky Lake.	clay-shale, calcareous shale, minor calcarenite, calcisiltite, and calcilutite	Lockhovian (Helderbergian)	Dunbar, 1919; Bassler and Moodey, 1943; e.g., Shimer and Shrock, 1944; Wilson, 1949; Strimple *in* Moore and Teichert, 1978
Rockhouse Shale Member, Ross Formation	8.04 km (5 miles) northwest of Lowryville, Hardin County, Tennessee, USA	calcisiltite, calcareous shale	Lockhovian (Helderbergian)	Dunbar, 1919; e.g., Dunbar, 1920; Ehrenberg, 1928; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Wilson, 1949; Strimple *in* Moore and Teichert, 1978
Rockhouse Shale Member, Ross Formation	8.04 km (5 miles) southeast of Savannah, Hardin County, Tennessee, USA	calcisiltite, calcareous shale	Lockhovian (Helderbergian)	e.g., Miller, 1889; Dunbar, 1919, 1920; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Wilson, 1949; Strimple *in* Moore and Teichert, 1978
E. dispansus?				

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Cravatt Member of the Bois d'Arc Formation, Hunton Group	near Clarita, Coal County, Oklahoma, USA (NW1/4 SW1/4 NW1/4 sec. 33, T. 1 S., R. 8 E., Wapanucka 7.5' Quadrangle)	shaly calcisiltite and calcilutite with beds of calcarenite	Lockhovian (Helderbergian)	e.g., Amsden, 1958; Frest et al., 1999; Parsley and Sumrall, 2007
Haragan Formation, Hunton Group	in outcrop adjacent to Wachita River, west of Dougherty, Murray County, Oklahoma, USA (center SW 1/4 sec. 11, T. 2 S., R. 2 E., Dougherty 7.5' Quadrangle)	shaly calcisiltite and calcilutite	Lockhovian (Helderbergian)	Frest et al., 1999; Parsley and Sumrall, 2007
E. pocilliformis				
Camden Formation	Whirl at the Buffalo River, 6.43 km (4 miles) north of Bakerville, Humphreys County, Tennessee, USA	shaly calcisiltite and calcilutite, chert	Lockhovian–Emsian (Helderbergian–?Deerparkian)	Foerste, 1903
Camden Formation?	Wells Creek Crater, Stewart County, Tennessee, USA	shaly calcisiltite and calcilutite, chert	Lockhovian–Emsian (Helderbergian–?Deerparkian)	Foerste, 1903; e.g., Dunbar, 1919; Springer, 1920; Goldring, 1923; Bassler and Moodey, 1943; Clement and Brett, 2015
E. pocilliformis?				

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Camden Formation?	Grandview, Bath Springs 7.5' Quadrangle, Hardin County, Tennessee, USA. This site is 12.87 km (8 miles) west of Clifton, Wayne County, Tennessee.	shaly calcisiltite and calcilutite, chert	Lockhovian–Emsian (Helderbergian–?Deerparkian)	Dunbar, 1919
Camden Formation?	Dry Creek, Hardin County, Tennessee, USA. This site is now 11.4 km (7.1 miles) west of Walnut Grove and underwater because the Tennessee Valley Authority has since created Pickwick Lake.	shaly calcisiltite and calcilutite, chert	Lockhovian–Emsian (Helderbergian–?Deerparkian)	Dunbar, 1919
E. dispansus				
1-2 m above the boundary of the Loděnice Limestone, Dvorce-Prokop Limestone Member, Praha Formation	Červený lom Quarry, Praha-Klukovice, Czech Republic	calcisiltite and calcilutite	Pragian (Helderbergian)	Chlupáč et al., 1985; Prokop, 1976; e.g., Prokop, 1987; Prokop and Petr, 1995b; Prokop and Turek, 2014
Dvorce-Prokop Limestone Member, Praha Formation	St. Prokop Quarries, Praha-Hlubočepy, Czech Republic	calcisiltite and calcilutite	Pragian (Helderbergian)	Chlupáč et al., 1985; e.g., Prokop, 1987; Prokop and Turek, 2014
Dvorce-Prokop Limestone Member, Praha Formation	Na Konvářce section at the roadcut, Praha-Smíchov, Czech Republic	calcisiltite and calcilutite	Pragian (Helderbergian)	Chlupáč et al., 1985; e.g., Prokop, 1987; Prokop and Turek, 2014

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Dvorce-Prokop Limestone Member, Praha Formation	Branická skála Quarry, Praha-Braník, Czech Republic	calcisiltite and calcilutite	Pragian (Helderbergian)	Chlupáč et al., 1985; e.g., Prokop, 1987; Prokop and Turek, 2014
Dvorce-Prokop Limestone Member, Praha Formation	U kantiny Quarry, Praha-Řeporyje, Czech Republic	calcisiltite and calcilutite	Pragian (Helderbergian)	Chlupáč et al., 1985; e.g., Prokop, 1987; Prokop and Turek, 2014
Koněprusy Limestone Member, Praha Formation	Čertovy schody - West Quarry, Czech Republic	calcarenite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop and Turek, 2014
Koněprusy Limestone Member, Praha Formation	Na Plešivci Quarry, Suchomasty, Czech Republic	calcarenite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop and Turek, 2014
Slivenec Limestone Member, Praha Formation	Na Konvářce Quarry, Praha-Smíchov, Czech Republic	calcarenite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop, 2013; Prokop and Turek, 2014
Slivenec Limestone Member, Praha Formation	western part of the Červený lom Quarry, Praha-Klukovice, Czech Republic	calcarenite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop, 2013; Prokop and Turek, 2014
Slivenec Limestone Member, Praha Formation	quarry by Zlíchov church, Praha-Zlíchov, Czech Republic	calcarenite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop, 2013; Prokop and Turek, 2014
Slivenec Limestone Member, Praha Formation	U kantiny Quarry, Praha-Řeporyje, Czech Republic	calcarenite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop, 2013; Prokop and Turek, 2014
Slivenec Limestone Member, Praha Formation	U Ohrady Quarry, Praha-Řeporyje, Czech Republic	calcarenite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop, 2013; Prokop and Turek, 2014

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Slivenec Limestone Member, Praha Formation	quarry in the Kačák Brook valley near its discharge into the Berounka River, Srbsko near Beroun, Czech Republic	calcarenite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop, 2013; Prokop and Turek, 2014
Loděnice Limestone Member, Praha Formation	Na Konvářce Quarry, Praha-Smíchov, Czech Republic	calcarenite, calcisiltite, and calcilutite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop, 2013; Prokop and Turek, 2014
Loděnice Limestone Member, Praha Formation	western part of the Červený lom Quarry, Praha-Klukovice, Czech Republic	calcarenite, calcisiltite, and calcilutite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop, 2013; Prokop and Turek, 2014
Loděnice Limestone Member, Praha Formation	quarry by Zlíchov church, Praha-Zlíchov, Czech Republic	calcarenite, calcisiltite, and calcilutite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop, 2013; Prokop and Turek, 2014
Loděnice Limestone Member, Praha Formation	U kantiny Quarry, Praha-Řeporyje, Czech Republic	calcarenite, calcisiltite, and calcilutite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop, 2013; Prokop and Turek, 2014
Loděnice Limestone Member, Praha Formation	U Ohrady Quarry, Praha-Řeporyje, Czech Republic	calcarenite, calcisiltite, and calcilutite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop, 2013; Prokop and Turek, 2014
Loděnice Limestone Member, Praha Formation	quarry in the Kačák Brook valley near its discharge into the Berounka River, Srbsko near Beroun, Czech Republic	calcarenite, calcisiltite, and calcilutite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop, 2013; Prokop and Turek, 2014
Koněprusy Limestone Member, Praha Formation	Císařský lom Quarry at the Zlatý kůň hill near Koněprusy, Czech Republic	calcarenite	Pragian (Helderbergian)	e.g., Prokop, 1987; Prokop and Petr, 1995a
E. sacculus				

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Taunus Quartzite Formation, Obersiegen Group	Nochern, Taunus, Rhenish Schiefergebirge, Germany	sandstone	Pragian (Helderbergian)	Kayser, 1885; Jaekel, 1899, 1914; Wanner, 1915; Bassler and Moodey, 1943; Gross Groß, 1948; e.g., LeMaître, 1958a; Prokop, 1976; Krebs, 1979; Ziegler, 1979
Taunus Quartzite Formation, Obersiegen Group	Singhofen, Taunus, Rhenish Schiefergebirge, Germany	sandstone	Pragian (Helderbergian)	Kayser, 1885; Jaekel, 1899, 1914; Wanner, 1915; Bassler and Moodey, 1943; Gross Groß, 1948; e.g., LeMaître, 1958a; Prokop, 1976; Krebs, 1979; Ziegler, 1979
Obere Siegen Formation, Obersiegen Group	Siegen, Siegerland, Rhenish Schiefergebirge, Germany	sandstone	Pragian (Helderbergian)	Kayser, 1885; Jaekel, 1899, 1914; Wanner, 1915; Bassler and Moodey, 1943; Gross Groß, 1948; e.g., LeMaître, 1958a; Prokop, 1976; Krebs, 1979; Ziegler, 1979

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Obere Siegen Formation, Obersiegen Group	Neunkirchen, Siegerland, Rhenish Schiefergebirge, Germany	sandstone	Pragian (Helderbergian)	Kayser, 1885; Jaekel, 1899, 1914; Wanner, 1915; Bassler and Moodey, 1943; Gross Groß, 1948; e.g., LeMaître, 1958a; Prokop, 1976; Krebs, 1979; Ziegler, 1979
Bovisand Formation, Meadfoot Group	Polyne Quarry, near Looe, Cornwall, England	mudstone, siltstone, sandstone, calcarenite	Pragian–Emsian (Helderbergian–?Deerparkian)	Green and Sherborn, 1906; e.g., Bather, 1928; Leveridge, 2011; Leveridge and Shail, 2011
Oriskany Sandstone	Washington County, Maryland, USA	quartz arenite	Emsian (Deerparkian)	e.g., Kirk, 1911; Shimer and Shrock, 1944; Amsden, 1951; Clement and Brett, 2015
Oriskany Sandstone	between Monterey and Strait Creek, US Route 220, Highland County, Virginia, USA	quartz arenite	Emsian (Deerparkian)	Kirk, 1911; Butts, 1940; Shimer and Shrock, 1944; Clement and Brett, 2015
Glenerie Formation, Tristates Group	Becraft Mountain, Hudson, Columbia County, New York, USA	siliceous calcarenite and calcisiltite; quartz pebble conglomerates with siliceous matrix	Emsian (Deerparkian)	Clarke, 1900, 1903; e.g., Springer, 1920; Goldring, 1923, 1931; Ehrenberg, 1928; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Clement and Brett, 2015

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Glenerie Formation, Tristates Group	Cuddebackville to Port Jervis, Orange County, New York, USA	siliceous calcarenite and calcisiltite; quartz pebble conglomerates with siliceous matrix	Emsian (Deerparkian)	Clarke, 1900; Goldring, 1931; e.g., Shimer and Shrock, 1944; Clement and Brett, 2015
Glenerie Formation, Tristates Group	Glenerie, 11.26 km (7 miles) north of Kingston, Ulster County, New York, USA	siliceous calcarenite and calcisiltite; quartz pebble conglomerates with siliceous matrix	Emsian (Deerparkian)	Clarke, 1900; Goldring, 1923, 1931; Ehrenberg, 1928; Bassler and Moodey, 1943; Chadwick, 1944; e.g., Shimer and Shrock, 1944; Clement and Brett, 2015
Oriskany Sandstone	Franklin, Pendleton County, West Virginia, USA	quartz arenite	Emsian (Deerparkian)	Rathbun, 1904; Kirk, 1911; Ohern, 1913; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Clement and Brett, 2015
Oriskany Sandstone	Knobly Mountain, near Cumberland, Allegany County, Maryland, USA	quartz arenite	Emsian (Deerparkian)	Kirk, 1911; Ohern, 1913; Bassler and Moodey, 1943; e.g., Shimer and Shrock, 1944; Clement and Brett, 2015
Oriskany Sandstone	east side Nicholas Mountain, Allegany County, Maryland, USA	quartz arenite	Emsian (Deerparkian)	e.g., Kirk, 1911; Ohern, 1913; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Clement and Brett, 2015

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Ridgeley Member, Old Port Formation	Sunbrook, Blair County, Pennsylvania, USA	cherty, silty mudstone and calcareous, siliceous siltstone	Emsian (Deerparkian)	e.g., Willard and Cleaves, 1938; Butts, 1945; Seilacher and MacClintock, 2005
Oriskany Sandstone	Cumberland, Allegany County, Maryland, USA	quartz arenite	Emsian (Deerparkian)	Hall, 1859; Wachsmuth and Springer, 1885, 1886; Miller, 1889; Clarke, 1900; e.g., Grabau and Shimer, 1910; Kirk, 1911; Springer, 1920; Goldring, 1923; Ehrenberg, 1928; Bassler and Moodey, 1943; Shimer and Shrock, 1944; Strimple *in* Moore and Teichert, 1978; Clement and Brett, 2015
Glenerie Formation?, Oriskany Group	Peter's Valley, Sussex County, New Jersey, USA	quartz pebble conglomerate and quartz sandstone	Emsian (Deerparkian)	Weller, 1900; Shimer and Shrock, 1944; Clement and Brett, 2015
Oriskany Sandstone	Knobly Mountain, Mineral County, West Virginia, USA	quartz arenite	Emsian (Deerparkian)	Kirk, 1911; Ohern, 1913; Swartz, 1913; Swartz et al., 1913; Shimer and Shrock, 1944; Clement and Brett, 2015

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Shriver Member, Old Port Formation	Lewistown, Mifflin County, Pennsylvania, USA	cherty, silty mudstone and calcareous, siliceous siltstone	Emsian (Deerparkian)	e.g., Willard and Cleaves, 1938; Cleaves, 1939; Swartz, 1939
Ridgeley Member, Old Port Formation	Hyndman, Bedford County, Pennsylvania, USA	quartz arenite	Emsian (Deerparkian)	e.g., Willard and Cleaves, 1938; Cleaves, 1939; Shimer and Shrock, 1944; Clement and Brett, 2015
Shriver Member, Old Port Formation	Mount Eagle, Centre County, Pennsylvania, USA	cherty, silty mudstone and calcareous, siliceous siltstone	Emsian (Deerparkian)	e.g., Willard and Cleaves, 1938; Cleaves, 1939; Swartz, 1939
Ridgeley Member, Old Port Formation	Montoursville, Lycoming County, Pennsylvania, USA	quartz arenite	Emsian (Deerparkian)	Cleaves, 1939; e.g., Shimer and Shrock, 1944; Clement and Brett, 2015
Edriocrinus cf. sacculus				
Little Saline Limestone	Little Saline Creek, Sainte Genevieve County, Missouri, USA	calcarenite	Emsian (Deerparkian)	Stewart *in* Branson, 1922; Bassler and Moodey, 1943; Clement and Brett, 2015
E. sacculus?				
Tarratine Formation lithologies	Greenlaw Pond 7.5' Quadrangle, Aroostook County, Maine, USA	sandstone, sandy limestone, siltstone, slate	Emsian (Deerparkian)	Boucot and Wilson, 1994
Seboomook Group	third cove west of large point 2.81 km (1.75 miles) southwest of Telos Dam, Telos Lake, Piscataquis County, Maine, USA	local conglomerate, calcareous fine-grained sandstone, siltstone, slate	Emsian (Deerparkian)	Hall, 1970; Kite and Kammer, 1988
E. dispansus				

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Chefar El Ahmar Formation	Erg Djemel, southeast of Ougarta, Béni Abbès, Béchar Province, Algeria	shale, silty sandstone, minor calcarenite?, calcisitite, calcilutite	Emsian (?Esopusian)	e.g., LeMaître, 1954, 1958a, b; Prokop, 1976; Boumendjel et al., 1997a, b; Le Menn, 1997; Paris et al., 1997; Plusquellec et al., 1997
about 1 m above the boundary with the Chapel Coral Horizon, Zlíchov Limestone Member, Zlíchov Formation	Červený lom Quarry, Praha-Klukovice, Czech Republic	calcisiltite and calcilutite	Emsian: Zlíchovian (Esopusian)	e.g., Prokop, 1987; Prokop and Petr, 1995b; Prokop and Turek, 2014
Edriocrinus sp.				
Kaplička Horizon at the base of the Zlíchov Limestone Member, Zlíchov Formation	U kapličky Quarry, Praha-Zlíchov, Czech Republic	calcirudite, calcarenite, calcisiltite, and calcilutite	Emsian: Zlíchovian (Esopusian)	e.g., Prokop, 1987; Prokop and Turek, 2014
Kaplička Horizon at the base of the Zlíchov Limestone Member, Zlíchov Formation	Hvížďalka Quarry, Lochkov, Czech Republic	calcirudite, calcarenite, calcisiltite, and calcilutite	Emsian: Zlíchovian (Esopusian)	e.g., Prokop, 1987; Prokop and Turek, 2014
E. dispansus				
Třebotov Limestone Member, Daleje-Třebotov Formation	Prastav Quarry, Praha-Holyně, Czech Republic	calcisiltite and calcilutite	Emsian: Dalejan (Southwoodian)	Prokop, 1976; e.g., Prokop, 1987; Prokop and Petr, 1995b; Prokop and Turek, 2014
Edriocrinus sp.				
Třebotov Limestone Member, Daleje-Třebotov Formation	U jezírka Quarry, Praha-Hlubočepy, Czech Republic	calcisiltite and calcilutite	Emsian: Dalejan (Southwoodian)	e.g., Prokop, 1987; Prokop and Turek, 2014

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Třebotov Limestone Member, Daleje-Třebotov Formation	section at the roadcut of the highway at Praha-Barrandov, Czech Republic	calcisiltite and calcilutite	Emsian: Dalejan (Southwoodian)	e.g., Prokop, 1987; Prokop and Turek, 2014
E. dispansus				
Choteč Limestone Member, Choteč Formation	section at the roadcut of the highway at Praha-Barrandov, Czech Republic	calcarenite, calcisiltite, and calcilutite	early Eifelian (Southwoodian)	e.g., Prokop, 1987; Prokop and Petr, 1995b
Edriocrinus sp.				
Choteč Limestone Member, Choteč Formation	Prastav Quarries, Praha-Holyně, Czech Republic	calcarenite, calcisiltite, calcilutite, calcareous shales	early Eifelian (Southwoodian)	e.g., Prokop, 1987; Prokop and Turek, 2014
E. dispansus				
4-5 m above the base of the Acanthopyge Limestone Member, Choteč Formation	abandoned quarry on the southern slope of the Zadní Kobyla hill, Koněprusy region, Czech Republic	calcarenite and calcisiltite	Eifelian (Southwoodian)	e.g., Prokop, 1987; Prokop and Turek, 2014
E. pyriformis				
Edgecliff? Moorehouse Members?, Onondaga Limestone	Eastman's Quarry southeast of Utica, near Litchfield, Oneida County, New York, USA. Eastman's Quarry no longer exists at this site.	Edgecliff: sandy conglomerate, calcarenite, silty calcareous shale, calcisiltite, calcilutite, shaly calcisiltite and calcilutite. Moorehouse: calcisiltite, calcareous shale, claystone, shaly calcisiltite and calcilutite	Eifelian (Southwoodian)	e.g., Hall, 1862; Wachsmuth and Springer, 1885, 1886; Miller, 1889; Springer, 1920; Goldring, 1923, 1938; Ehrenberg, 1928; Bassler and Moodey, 1943; Shimer and Shrock, 1944

Table 6.1 (continued)

Unit	Location	Lithology	Stage	Relevant references
Edgecliff? Moorehouse Members?, Onondaga Limestone	Babcock Hill, Bridgewater, Oneida County, New York, USA	Edgecliff: sandy conglomerate, calcarenite, silty calcareous shale, calcisiltite, calcilutite, shaly calcisiltite and calcilutite. Moorehouse: calcisiltite, calcareous shale, claystone, shaly calcisiltite and calcilutite	Eifelian (Southwoodian)	e.g., Goldring, 1923, 1938; Rickard and Zenger, 1964; Clement and Broadhead, 1994; Clement and Brett, 2015
Edgecliff? Nedrow Members?, Onondaga Limestone	Williamsville, Erie County, New York, USA	Edgecliff: sandy conglomerate, calcarenite, silty calcareous shale, calcisiltite, calcilutite, shaly calcisiltite and calcilutite. Nedrow: K-bentonite?, calcisiltite, calcilutite, shaly calcisiltite and calcilutite, calcareous shale, shale	Eifelian (Southwoodian)	Goldring, 1938; Bassler and Moodey, 1943; e.g., Clement and Broadhead, 1994; Clement and Brett, 2015
E. pyriformis?				
Moorehouse Member, Onondaga Limestone	near Oaks Corners, north end of Seneca Lake, Ontario County, New York, USA	calcisiltite, calcareous shale, claystone, shaly calcisiltite and calcilutite	Eifelian (Southwoodian)	Brett and ver Straeten, 1994; e.g., Clement and Broadhead, 1994; Clement and Brett, 2015

Table 6.2 Species and lithologies

Species	Lithologies
E. pocilliformis	calcisiltite and calcilutite; shaly calcisiltite and calcilutite; clay-shale, calcareous shale, minor calcarenite with calcisiltite and calcilutite; calcarenite, calcisiltite, and calcilutite; calcarenite interbedded with shale; calcisiltite, calcareous shale; silty shale, shaly calcisiltite and calcilutite, calcareous, siliceous, laminated shale; shaly calcisiltite and calcilutite, chert
E. pocilliformis?	shaly calcisiltite and calcilutite
E. pocilliformis?	shaly calcisiltite and calcilutite, chert
E. sacculus	sandstone; mudstone, siltstone, sandstone, calcarenite; siliceous calcarenite and calcisiltite, quartz pebble conglomerates with siliceous matrix; quartz pebble conglomerate and quartz sandstone; quartz arenite; cherty, silty mudstone and calcareous, siliceous siltstone
Edriocrinus cf. sacculus	calcarenite
E. sacculus?	sandstone, sandy limestone, siltstone, slate; local conglomerate, calcareous fine-grained sandstone, siltstone, slate
E. pyriformis	sandy conglomerate, calcarenite, silty calcareous shale, calcisiltite, calcilutite, shaly calcisiltite and calcilutite; calcisiltite, calcareous shale, claystone, shaly calcisiltite and calcilutite; K-bentonite?, calcisiltite, calcilutite, shaly calcisiltite and calcilutite, calcareous shale, shale
Edriocrinus cf. pyriformis	calcarenite interbedded with shale
E. pyriformis?	calcisiltite, calcareous shale, claystone, shaly calcisiltite and calcilutite
E. dispansus	shaly calcisiltite and calcilutite; clay-shale, calcareous shale, minor calcarenite with calcisiltite and calcilutite; calcarenite interbedded with shale; calcisiltite, calcareous shale; calcisiltite and calcilutite; calcarenite; calcarenite, calcisiltite, and calcilutite; shale, silty sandstone, minor calcarenite?, calcisitite, calcilutite; calcarenite and calcisiltite
E. dispansus?	shaly calcisiltite and calcilutite with beds of calcarenite; shaly calcisiltite and calcilutite
Edriocrinus sp.	calcirudite, calcarenite, calcisiltite, and calcilutite; calcisiltite and calcilutite; calcarenite, calcisiltite, calcilutite, calcareous shales

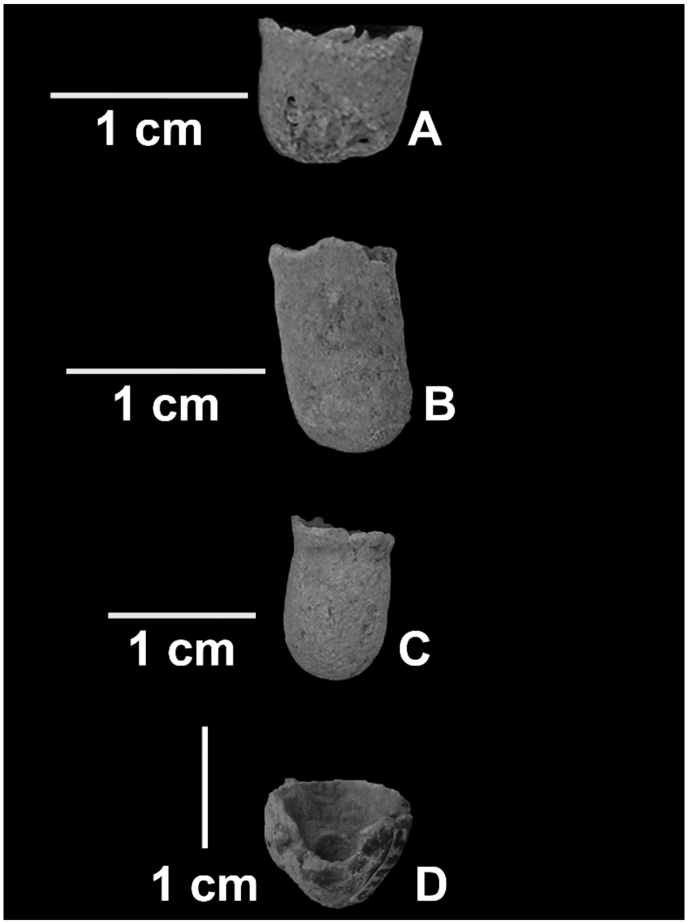

Figure 6.1 Ecophenotypes of *E. pocilliformis*. A: Distally flattened, USNM 1902. B: Distally rounded, USNM 1902. C: Distally rounded with a flared collar, USNM 1902. D: Distally tapered and rounded, C2965.

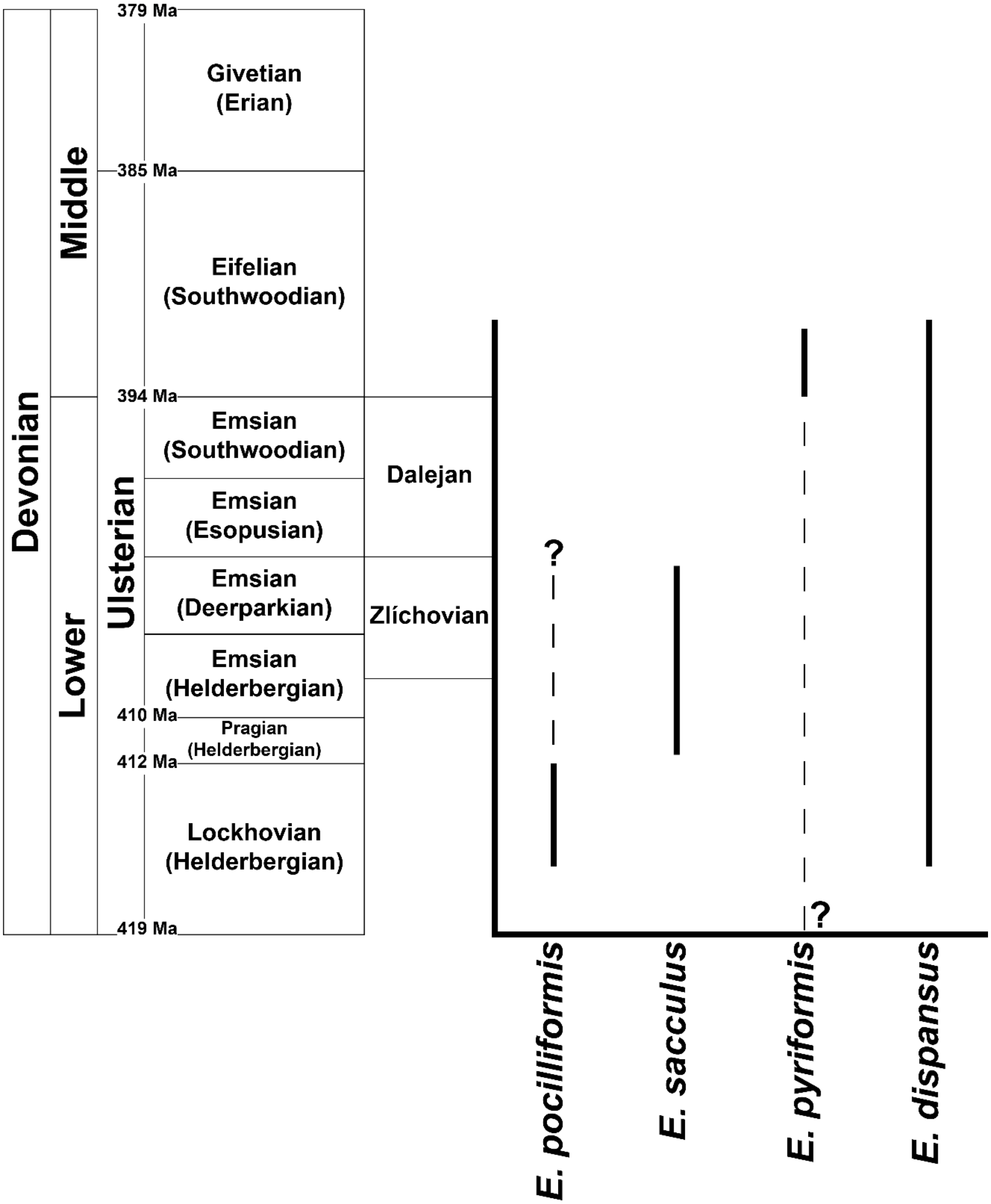

Figure 6.2 Geologic range of *Edriocrinus* species.

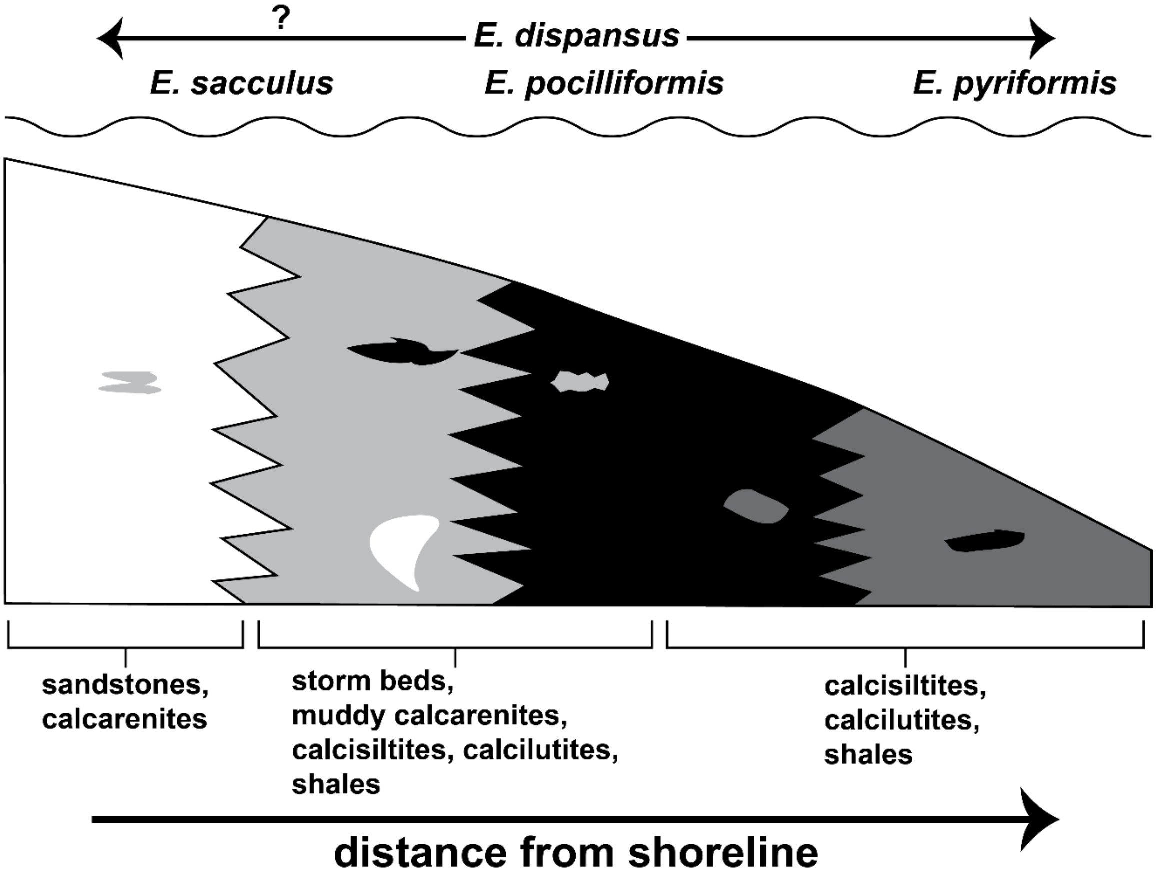

Figure 6.3 Possible environments of *Edriocrinus* species.

CHAPTER 7. CONCLUSIONS

The aim of this study is to provide a modern classification and understanding of the enigmatic stemless Paleozoic crinoid *Edriocrinus*. Most of the previous work regarding this genus was done before the context of plate tectonics and systematics existed. Awareness that fossils should not be studied in isolation from such concepts and their underlying patterns and processes has enabled development of a more holistic view of *Edriocrinus*, summarized as follows.

(1) *Edriocrinus* is restricted to Early–early Middle Devonian time (Ulsterian; middle Lockhovian–early Eifelian) at ~416.2 Ma?—~391 Ma. within the *Ancyrodelloides carlsi–Polygnathus costatus* conodont zones. (2) The previous, problematic classification that associated *Edriocrinus* with the flexibles was only based on a few incompletely preserved arms from one species and excluded the better, more diagnostic traits of the arms and cups, which are more reliably preserved. (3) The more diagnostic traits that distinguish *Edriocrinus* from flexible crinoids include: a dorsal cup with firmly bound plates, presence of five, high infrabasals which are visible from the side in unattached forms, lack of patelloid processes in the arms, presence of straight muscular articulation on radial facets, presence of brachials that are rigidly attached to and free above the radials, and presence of muscular articulation between brachials. These traits indicate that *Edriocrinus* is a eucladid. (4) Additionally, presence of five infrabasals, possibly fused, three-to-no anal plates in the cup, an anal sac which is absent or poorly developed, and non-pinnulate arms with rectangular uniserial brachials suggest that *Edriocrinus* is a dendrocrinid. (5) Many of the fourteen previous *Edriocrinus* species are probably ecophenotypes of the same species, resulting in an excessively split genus. New evaluation of species taxobases

suggests that the 14 previous species can be synonymized into four: *E. pocilliformis, E. sacculus, E. pyriformis,* and *E. dispansus.* (6) *E. pocilliformis, E. sacculus,* and *E. dispansus* exhibit ecophenotypic variations in cup morphology that probably developed as responses to varying environmental conditions. Previous workers believed these variations to be taxobases that could define new species, but as homoplasic characters they lack taxonomic value. (7) *Edriocrinus* lived in parts of the Eastern Americas biogeographic realm, from the south-central to north-central USA, and parts of the Old World realm, from northeastern USA, southern England, west-central Germany, northern Algeria, and the central Czech Republic. During Early–Middle Devonian time, these areas surrounded the Rheic Ocean at about 25°–35° south latitude, in subtropical to warm-temperate climatic zones, where large-scale oceanic currents could have transported crinoid larvae between realms. (8) The phenotypic plasticity of *Edriocrinus* evidently enabled most species to live in a variety of shallow, agitated environments, favorable to the deposition of both clastics and carbonates, within the generally regressive setting of the Lower to Middle Devonian. *E. pocilliformis* occurs in calcarenites, calcisiltites, calcilutites, shales, and cherts, indicating life in both high- and low-energy settings. Most *E. sacculus* occur in sandstones, quartz arenites, and calcarenites associated with high-energy settings, but a few are known from siltstones, slates, silty mudstones, and calcisiltites associated with lower-energy settings. *E. pyriformis* occurs in calcisiltites, calcilutites, shales, and claystones, and probably lived in low-energy settings. *E. dispansus* is known from rocks of both low- and high-energy settings, namely shales, calcilutites, calcisiltites, silty sandstones, and calcarenites. *E. dispansus* may have lived in low-energy settings, whereas *E. dispansus* preserved in high-energy settings may have been transported. (9) The unattached *E.*

pocilliformis was epifaunal or semi-infaunal and possibly mobile, consistent with the model of *Agassizocrinus*, using its arms to move like *E. sacculus*. Unattached *E. sacculus* inserted their cups into mobile sands to assume a semi-infaunal life mode, crawling to move, also like *Agassizocrinus*. Attached forms of *E. sacculus* were epifaunal encrusters on hard substrates, including other organisms such as brachiopods. *E. pyriformis* attached itself with a "false stem" derived from the elongated infrabasal and basal circlets of the cup, suggesting a semi-infaunal life mode. The epifaunal *E. dispansus* attached to hard substrates, sometimes encrusting the hard parts of various other organisms, or the broad cup rested on soft, muddier substrates. Attachment to any stationary host, living or dead, suggests a stationary lifestyle. In contrast, attached, epiplanktic *E. dispansus* may have remained pelagic throughout their lives, "hitchhiking" on living, floating hosts such as cephalopods and the loboliths of *Scyphocrinites*. (10) Early Eifelian carbonate rocks from the Czech Republic include siliciclastics and black shales, likely deposited during global tectonic and eustatic events that were factors in anoxia during the Chotec Event. Similarly, slightly younger North American rocks change from limestones to dark, calcareous shales and reflect eustatic sea-level rise and resulting deepening and hypoxia associated with the Bakoven Event. The changing sea levels and oxygen levels during the Chotec and Bakoven Events may have facilitated the extinction of *Edriocrinus*.

REFERENCES

Amsden, T.W., 1951, Paleontology of Washington County: Department of Geology, Mines, and Water Resources, State of Maryland, The Physical Features of Washington County, p. 98–124.

Amsden, T.W., 1957, Stratigraphy and paleontology of the Hunton Group in the Arbuckle Mountain region, part I—introduction to stratigraphy: Oklahoma Geological Survey Circular, v. 44, 57 p.

Amsden, T.W., 1958, Stratigraphy and paleontology of the Hunton Group in the Arbuckle Mountain region, part V—Bois d'Arc articulate brachiopods: Oklahoma Geological Survey Bulletin, v. 82, 110 p.

Ausich, W.I., and Meyer, D.L., 1992, Crinoidea Flexibilia (Echinodermata) from the Fort Payne Formation (Lower Mississippian; Kentucky and Tennessee): Journal of Paleontology, v. 66, p. 825–838.

Bábek, O., Faměra, M., Hladil, J., Kapusta, J., Weinerová, H., Šimíček, D., Slavík, L., and Ďurišová, J., 2018, Origin of red pelagic carbonates as an interplay of global climate and local basin factors: insight from the Lower Devonian of the Prague Basin, Czech Republic: Sedimentary Geology, v. 364, p. 71–88.

Bassler, R.S., and Moodey, M.W., 1943, Bibliographic and Faunal Index of Paleozoic Pelmatozoan Echinoderms: Geological Society of America Special Paper 45, 734 p.

Bather, F.A., 1896, On *Uintacrinus*: a morphological study: Proceedings of the Zoological Society of London, v. 1895, p. 974–1004.

Bather, F.A., 1899, A phylogenetic classification of the Pelmatozoa, *in* Report of the Sixty-eighth Meeting of the British Association for the Advancement of Science held at Bristol in September 1898: London, John Murray, p. 916–923.

Bather, F.A., 1900, The Echinoderma: London, Adam and Charles Black, A Treatise on Zoology, Part III, 344 p.

Bather, F.A., 1928, Anniversary address of the president: the fossil and its environment: The Quarterly Journal of the Geological Society of London, v. 84, p. lxi–xcviii.

Baumiller, T.K., Gahn, F.J., Hess, H., Messing, C.G., 2008, Taphonomy as an indicator of behavior among fossil crinoids, *in* Ausich, W.I., and Webster, G.D., eds., Echinoderm Paleobiology: Bloomington and Indianapolis, Indiana University Press, p. 7–20.

Baumiller, T.K., Salamon, M.A., Gorzelak, P., Mooi, R., Messing, C.G., Gahn, F.J., 2010, Post-Paleozoic crinoid radiation in response to benthic predation preceded the Mesozoic marine revolution: Proceedings of the National Academy of Sciences, v. 107, p. 5893–5896.

Becker, R.T., Marshall, J.E.A., and Da Silva, A.-C., 2020, The Devonian period, *in* Gradstein, F.M, Ogg, J.G, Schmitz, M.D, and Ogg, G.M., eds., Geologic Time Scale 2020 v. 2: Amsterdam, Elsevier, p. 733–810.

Boucot, A.J., 1985, Late Silurian–early Devonian biogeography, provincialism, evolution, and extinction: Philosophical Transactions of the Royal Society, Series B, Biological Sciences, v. 309, p. 323–339.

Boucot, A.J., and Wilson, R.A., 1994, Origin and early radiation of terebratuloid brachiopods: thoughts provoked by *Prorensselaeria* and *Nanothyris*: Journal of Paleontology, v. 68, p. 1002–1025.

Boumendjel, K., Brice, D., Copper, P., Gourvennec, R., Jahnke, H., Lardeux, H., Le Menn, J., Melou, M., Morzadec, P., Paris, F., Plusquellec, Y., and Rachebœuf, P., 1997, Les faunes du Dévonien de l'Ougarta (Sahara occidental, Algérie): Annales de Société Géologique du Nord, v. 5, p. 89–116.

Boumendjel, K., Morzadec, P., Paris, F., and Plusquellec, Y., 1997, Le Dévonien de l'Ougarta (Sahara occidental, Algérie): Annales de Société Géologique du Nord, v. 5, p. 73–87.

Breimer, A., 1978, Autecology, *in* Moore, R.C. and Teichert, C., eds., Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Volume 1: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. T331–T343.

Brett, C.E., and ver Straeten, C.A., 1994, Stratigraphy and facies relationships of the Eifelian Onondaga Limestone (Middle Devonian) in western and west central New York state, *in* Brett, C.E., and Scatterday, J., eds., Field Trip Guidebook, New York State Geological Association, 66th Annual Meeting: Rochester, New York State Geological Association, p.221–269.

Brett, C.E., Moffat, H.A., and Taylor, W.L., 1997, Echinoderm taphonomy, taphofacies, and Lagerstätten, *in* Waters, J.A., and Maples, C.G., eds., Geobiology of Echinoderms: Paleontological Society Papers, v. 3, p. 147–190.

Broadhead, T.W., Capaccioli, D.A., McComb, R., Reid, S.R., and Walker, K.R., 1988, Late Silurian and Early Devonian marine sedimentation near the southern margin of the North American craton, *in* McMillan, N.J, Embry, A.F., and Glass, D.J., eds., Devonian of the World: Proceedings of the Second International Symposium on the Devonian System, volume II: sedimentation: Canadian Society of Petroleum Geologists Memoir 14, p. 197–208.

Brower, J.C., 1978, Camerates, *in* Moore, R.C. and Teichert, C., eds., Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Volume 1: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. T244–T263.

Brower, J.C., 1987, The relations between allometry, phylogeny, and functional morphology in some calceocrinid crinoids: Journal of Paleontology, v. 61, p. 999–1032.

Buggisch, W., and Mann, U., 2004, Carbon isotope stratigraphy of Lockhovian to Eifelian limestones from the Devonian of central and southern Europe: International Journal of Earth Sciences, v. 93, p. 521–541.

Butts, C., 1940, Geology of the Appalachian Valley in Virginia Part I—geologic text and illustrations: Virginia Geological Survey Bulletin, v. 52, 568 p.

Butts, C., 1945, Description of the Hollidaysburg and Huntingdon Quadrangles: U.S. Geological Survey Geologic Atlas of the United States, Folio 227.

Butts, C., and Edmundson, R.S., 1963, Geologic map, Frederick County, Virginia: Virginia Division of Mineral Resources, scale 1:62,500, 2 sheets, 142 p. text.

Carlson, M.P., Nodine-Zeller, D.E., Thompson, T.L., and Witzke, B.J., 1987, Correlation of stratigraphic units of North America (COSUNA) Project: Mid-continent region: Tulsa, Oklahoma, American Association of Petroleum Geologists/Datapages Miscellaneous Series, 1 sheet.

Carpenter, P.H., 1887, On crinoids and blastoids: Proceedings of the Geologists' Association, v. 10, p. 19–28.

Chadwick, G.H., 1944, Geologic map of the Catskill and Kaaterskill Quadrangles: New York State Museum Bulletin 336, scale 1:62,500, 1 sheet, 251 p. text.

Chlupáč, I., 1988, The Devonian of Czechoslovakia and its stratigraphic significance, *in* McMillan, N.J, Embry, A.F., and Glass, D.J., eds., Devonian of the World: Proceedings of the Second International Symposium on the Devonian System, volume I: regional syntheses: Canadian Society of Petroleum Geologists Memoir 14, p. 481–497.

Chlupáč, I., 2003, Comments on facies development and stratigraphy of the Devonian, Barrandian area, Czech Republic: Bulletin of Geosciences, v. 78, p. 299–312.

Chlupáč, I., Lukeš, P., Paris, F., and Schönlaub, H.P., 1985, The Lockhovian-Pragian boundary in the Lower Devonian of the Barrandian area (Czechoslovakia): Jahrbuch der Geologische Bundesanstalt, v. 128, p. 9–41.

Chlupáč, I., and Kukal, Z., 1988, Possible global events and the stratigraphy of the Palaeozoic of the Barrandian (Cambrian–Middle Devonian, Czechoslovakia): Sborník Geologických Věd Geologie, v. 43, p. 83–146.

Clarke, J.M., 1900, The Oriskany fauna of Becraft Mountain, Columbia County, N.Y.: Memoir of the New York State Museum, v. 3, 128 p.

Clarke, J.M., 1903, Paleontology 8, catalogue of type specimens of Paleozoic fossils in New York State Museum: New York State Museum Bulletin, v. 65, 847 p.

Cleaves, A.B., 1939, The Oriskany Group: The Devonian of Pennsylvania: Pennsylvania Geological Survey Bulletin, v. G 19, p. 92–130.

Cleaves, E.T., Edwards, J., Jr., and Glaser, J.D., 1968, Geologic map of Maryland: Maryland Geological Survey, scale 1:250,000, 1 sheet.

Clement, C.R., and Brett, C.E., 2015, Echinoderm faunas of the Decatur Limestone and Ross Formation (Upper Silurian to Lower Devonian) of west-central Tennessee: Bulletins of American Paleontology, no. 388, 118 p.

Clement, C.R., and Broadhead, T.W., 1994, Biostratigraphy and biogeography of Late Silurian–Early Devonian echinoderms: New York State Museum Bulletin, v. 481, p. 45–54.

Cloos, E., 1951, Stratigraphy of sedimentary rocks of Washington County: Department of Geology, Mines, and Water Resources, State of Maryland, The Physical Features of Washington County, p. 17–94.

Copper, P., 2002, Silurian and Devonian reefs: 80 million years of global greenhouse between two ice ages, *in* Kiessling, W., Flügel, E., and Golonka, J., eds., Phanerozoic Reef Patterns: Tulsa, SEPM (Society for Sedimentary Geology) Special Publication 72, p. 181–238.

Davis, K., no date, Lower Devonian fossils of Tennessee: Memphis, Tennessee, Memphis Pink Palace Museum, 39 p.

Deline, B., and Thomka, J.R., 2017, The role of preservation on the quantification of morphology and patterns of disparity within Paleozoic echinoderms: Journal of Paleontology, v. 91, p. 618–632.

DeSantis, M.K., and Brett, C.E., 2011, Late Eifelian (Middle Devonian) biocrises: Timing and signature of the pre-Kačák Bakoven and Stony Hollow Events in eastern North America: Palaeogeography, Palaeoclimatology, Palaeoecology, v. 304, p. 113–135.

Diecchio, R.J., Jones, S.E., and Dennison, J.M., 1984, Oriskany Sandstone—regional stratigraphic relationships and production trends: West Virginia Geological and Economic Survey Map-WV17, scale 1:1,000,000, 8 sheets.

Donovan, S.K., 2006, Comment: Crinoid anchoring strategies for soft-bottom dwelling (Seilacher and MacClintock, 2005): Palaios, v. 21, p. 397–399.

Donovan, S.K., and Pawson, D.L., 2008, A new species of the sessile crinoid *Holopus* d'Orbigny from the tropical western Atlantic, with comments on holopodid ecology (Echinodermata: Crinoidea: Holopodidae): Zootaxa, v. 17, p. 31–38.

d'Orbigny, A., 1837, Mémoire sur une seconde espèce vivante de la famille des crinoïdes ou Encrines, servant de type au nouveau genre Holope (*Holopus*): Magasin de Zoologie, v. 7, no. 10, p. 1–8.

Drake, A.A., Jr., Volkert, R.A., Monteverde, D.H., Herman, G.C., Houghton, H.F., Parker, R.A., and Dalton, R.F., 1996, Bedrock geologic map of northern New Jersey: U.S. Geological Survey Miscellaneous Investigations Series Map I-2540-A, scale 1:100,000, 2 sheets, 7 p. text.

Dunbar, C.O., 1919, Stratigraphy and correlation of the Devonian of western Tennessee: State of Tennessee State Geological Survey Bulletin, v.21, 127 p.

Dunbar, C.O., 1920, New species of Devonian fossils from western Tennessee: Transactions of the Connecticut Academy of Arts and Sciences, v. XXIII, p. 109–158.

Ehrenberg, K., 1928, Palaeobiologische untersuchungen über die gattung *Edriocrinus*: Palaeobiologica, v. 1, p. 61–78.

Epstein, J.B., 1989, Geologic map of Cherry and Godfrey Ridges in the Saylorsburg, Stroudsburg, and East Stroudsburg Quadrangles, Monroe County, Pennsylvania: U.S. Geological Survey Miscellaneous Investigations Series Map I-1422, scale 1:8,000, 2 sheets.

Ettensohn, F.R., 1975, The autecology of *Agassizocrinus lobatus*: Journal of Paleontology, v. 49, p. 1044–1061.

Ettensohn, F.R., 1980, *Paragassizocrinus*: systematics, phylogeny, and ecology: Journal of Paleontology, v. 54, p. 978–1007.

Ettensohn, F.R., 1981, A case for substrate influence on infrabasal-cone morphology of two Paleozoic stemless crinoid genera from eastern Kentucky: Southeastern Geology, v. 22, p. 169–175.

Ettensohn, F. R., 1984, Unattached Paleozoic stemless crinoids as environmental indices: Géobios, v. 17, supplement 1, p. 63–68.

Ettensohn, F.R., 1985, The Catskill delta complex and the Acadian orogeny: a model, *in* Woodrow, D.L., and Sevon, W.D., eds., The Catskill Delta: Geological Society of America Special Paper 201, p. 39–49.

Ettensohn, F.R., 2008, The Appalachian foreland basin in eastern United States, *in* Miall, A.D., ed., The Sedimentary Basins of the United States and Canada: Sedimentary Basins of the World, v. 5: Amsterdam, Elsevier, p. 105–179.

Foerste, A., 1903, Silurian and Devonian limestones of western Tennessee: The Journal of Geology, v. 11, p. 679–715.

Frest, T.J., Brett, C.E., and Witzke, B.J., 1999, Caradocian–Gedinnian echinoderm associations of central and eastern North America, *in* Boucot, A.J., and Lawson, J.D., eds., Paleocommunities—A Case Study from the Silurian and Lower Devonian: Cambridge and New York, Cambridge University Press, p. 638–783.

Goldring, W., 1923, The Devonian crinoids of the state of New York: New York State Museum Memoir, v. 16, 670 p.

Goldring, W., 1931, Handbook of paleontology for beginners and amateurs, part 2: the formations: New York State Museum Handbook, v. 10, 488 p.

Goldring, W., 1938, Additional notes on previously described Devonian crinoids: New York State Museum Bulletin, v. 315, p. 77–83.

Gorzelak, P., Salamon, M.A., Baumiller, T.K., 2012, Predator-induced macroevolutionary trends in Mesozoic crinoids: Proceedings of the National Academy of Sciences, v. 109, p. 7004–7007.

Grabau, A.W., and Shimer, H.W., 1910, North American Index Fossils, v. II: New York, A.G. Seiler and Company, 909 p.

Green, U., and Sherborn, C.D., 1906, Lists of Wenlockian fossils from Porthluney, Cornwall; Ludlowian fossils from Porthalla; and Taunusian fossils from Polyne Quarry, near Looe, Cornwall: The Geological Magazine, v. III, p. 33–35.

Groß, K., 1948, Ein neuer fund von *Lodanella mira* Kayser im Unterdevon des Siegerlandes: Neues Jahrbuch für Geologie und Paläontologie Monatshefte Abteilungen B, Jahrgang 1945–1948, v. 4, p. 40–42.

Hall, B.A., 1970, Stratigraphy of the southern end of the Munsungun Anticlinorium, Maine: Maine Geological Survey Bulletin, v. 22, 63 p.

Hall, J., 1852, Palaeontology of New-York. volume II: Natural History of New York, v. 6, 362 p.

Hall, J., 1858, *in* Silliman, B., Silliman, B., Jr., and Dana, J.D., eds., Scientific intelligence, Crinoids of New York: The American Journal of Science and Arts, v. XXV, p. 277–279.

Hall, J., 1859, Palaeontology: volume III: Geological Survey of New-York Natural History of New York, v. 6, 533 p.

Hall, J., 1862, Preliminary notice of some of the species of Crinoidea known in the Upper Helderberg and Hamilton Groups of New-York: Fifteenth Annual Report of the Regents of the University of the State of New-York on the Condition of the State Cabinet of Natural History, and the Historical and Antiquarian Collection Annexed Thereto, p. 115–153.

Harrison, R.W., 1999, Geologic map of the Thebes Quadrangle, Illinois and Missouri: U.S. Geological Survey Geologic Quadrangle Map GQ-1779, scale 1:24,000, 1 sheet

Heckel, P.H., and Witzke, B.J., 1979, Devonian world palaeogeography determined from distribution of carbonates and related lithic palaeoclimatic indicators, *in* House, M.R., Scrutton, C.T., and Bassett, M.G., eds., The Devonian System: London, The Palaeontological Association, Special Papers in Palaeontology 23, p. 99–123.

Hess, H., 2011, Cyrtocrinida, *in* Selden, P.A., ed., Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Revised, Crinoidea, Volume 3: Lawrence, Kansas, The University of Kansas Paleontological Institute, p. 180–206.

Hladil, J., 1988, Structure and microfacies of Middle and Upper Devonian carbonate buildups in Moravia, Czechoslovakia, *in* McMillan, N.J, Embry, A.F., and Glass, D.J., eds., Devonian of the World: Proceedings of the Second International Symposium on the Devonian System, volume II: sedimentation: Canadian Society of Petroleum Geologists Memoir 14, p. 607–618.

Hollick, L.M., Shail, R.K., and Leveridge, B.E., 2006, Devonian rift-related sedimentation and Variscan tectonics—new data on the Looe and Gramscatho Basins from the resurvey of the Newquay district: Geoscience in South-West England, v. 11, p. 191–198.

International Commission on Zoological Nomenclature (ICZN), 1999, International Code of Zoological Nomenclature: London, The International Trust for Zoological Nomenclature 1999, 4th ed., 106 p.

Jaekel, O., 1894, Die morphogenie und phylogenie der crinoiden, *in* Sitzungs-Berichte der Gesellschaft Naturforschender Freunde zu Berlin: Berlin, R. Friedländer and Son, p. 101–146.

Jaekel, O., 1899, Stammesgeschichte der Pelmatozoen, v. 1, thecoidea und cystoidea: Berlin, Julius Springer, 441 p.

Jaekel, O., 1914, *Lodanella mira*, ein Edriocrinidae: Palaeontologische Zeitschrift, v. 1, p. 382–385.

Janevski, G. A., and Baumiller, T. K., 2010, Could a stalked crinoid swim? A biomechanical model and characteristics of swimming crinoids: Palaios, v. 25, p. 588–596.

Kayser, E., 1885, *Lodanella mira*, eine unterdevonische spongie: Zeitschrift der Deutschen Geologischen Gesellschaft, v. 37, p. 207–213.

Kesling, R.V., 1967, Cystoids, *in* Moore, R.C., ed., Treatise on Invertebrate Paleontology, Part S, Echinodermata 1, Volume 1: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. S85–S268.

Kesling, R.V., and Mintz, L.W., 1961, Notes on *Lepadocystis moorei* (Meek) an Upper Ordovician callocystitid cystoid: Contributions from the Museum of Paleontology, The University of Michigan, v. XVII, p. 123–148.

Keyes, C.R., 1894, Paleontology of Missouri (Part I): Missouri Geological Survey, v. IV, 271 p.

Kirk, E., 1911, The structure and relationships of certain eleutherozoic Pelmatozoa: Proceedings of the United States National Museum, v. 41, 137 p.

Kite, J.S., and Kammer, T.W., 1988, Occurrence of the crinoid *Rhodocrinites nortoni* (Goldring) from the Lower Devonian Seboomook Formation in the Telos Lake area, north-central Maine: Studies in Maine Geology, v. 1, p. 101–108.

Koptíková, L., 2011, Precise position of the Basal Choteč event and evolution of sedimentary environments near the Lower–Middle Devonian boundary: the magnetic susceptibility, gamma-ray spectrometric, lithological, and geochemical record of the Prague Synform (Czech Republic): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 304, p. 96–112.

Koptíková, L., Hladil, J., Slavík, L., Čejchan, P., and Bábek, O., 2010, Fine-grained non-carbonate particles embedded in neritic to pelagic limestones (Lockhovian to Emsian, Prague Synform, Czech Republic): composition, provenance and links to magnetic susceptibility and gamma-ray logs: Geologica Belgica, v. 13, p. 407–430.

Krebs, W., 1979, Devonian basinal facies, *in* House, M.R., Scrutton, C.T., and Bassett, M.G., eds., The Devonian System: London, The Palaeontological Association, Special Papers in Palaeontology 23, p. 125–139.

Lane, N.G., 1989, Some hypotheses concerning fossil crinoids, *in* Lane, N.G., ed., Workshop on fossil crinoids: Washington, D.C., p. 25–30.

Lane, N.G., and Moore, R.C., 1978, Suborder Cyathocrinina Bather, 1899, *in* Moore, R.C. and Teichert, C., eds., Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Volume 2: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. T578–T606.

Laporte, L.F., 1969, Recognition of a transgressive carbonate sequence within an epeiric sea: Helderberg Group (Lower Devonian) of New York state, *in* Friedman, G.M., ed., Depositional Environments in Carbonate Rocks: Tulsa, SEPM (Society for Sedimentary Geology) Special Publication 14, p. 98–119.

Le Maître, D., 1954, Échinodermes nouveaux du Dévonien Sud-Oranais: Comptes Rendus Hebdomadaires des Séances de l'Académie des Sciences, v. 238, p. 2107–2108.

Le Maître, D., 1958a, Contribution a l’étude des faunes Dévoniennes d’Afrique du nord I: Échinodermes: Publications du Service de la Carte Géologique de l’Algérie Bulletin, v. 20, p. 113–154.

Le Maître, D., 1958b, Crinoïdes du Dévonien d’Afrique du nord: Compte Rendu Sommaire des Séances de la Société Géologique de France, v. 14, p. 344–346.

Le Menn, J., 1997, Crinoïdes Devoniens d’Afrique du nord: revision systematique et affinites paleobiogeographiques: Annales de Société Géologique du Nord, v. 5, p. 129–139.

Leveridge, B.E., 2011, The Looe, South Devon and Tavy basins: the Devonian rifted passive margin successions: Proceedings of the Geologists’ Association, v. 122, p. 616–717.

Leveridge, B.E., and Shail, R.K., 2011, The marine Devonian stratigraphy of Great Britain: Proceedings of the Geologists’ Association, v. 122, p. 540–567.

Limam, H., Mehadji, A.O., and Bendella, M., 2021, The Chefar El Ahmar Formation (late Emsian–Frasnian Ib) in the Marhouma section (Saoura, Algerian Sahara): insights from ichnology and sedimentology: Arabian Journal of Geosciences, v. 14, doi: 10.1007/s12517-021-06669-4.

Marsaglia, K.M., and Klein, G.D., 1983, The paleogeography of Paleozoic and Mesozoic storm depositional systems: The Journal of Geology, v. 91, p. 117–142.

McIntosh, G., 1981, *Apurocrinus sucrei*, a new genus and species of camerate crinoid from the Lower Devonian of Bolivia: Journal of Paleontology, v. 55, p. 948–952.

Meek, F.B., and Worthen A.H., 1868, Geology and paleontology: Geological Survey of Illinois, v. III, 574 p.

Mehadji, A.O., Elmi, S., Rachebœuf, P., and Mekahli, L., 2004, Caractéristiques et signification d'un niveau coquillier majeur à brachiopodes, marqueur événementiel dans l'évolution Dévonienne de la Saoura (Sahara du Nord-Ouest, Algérie): Comptes Rendus Geoscience, v. 336, p. 1283–1292.

Meyer, D.L., Ausich, W.I., and Terry, R.E., 1989, Comparative taphonomy of echinoderms in carbonate facies: Fort Payne Formation (Lower Mississippian) of Kentucky and Tennessee: Palaios, v. 4, p. 533–552.

Miller, J.S., 1821, A natural history of the Crinoidea, or lily-shaped animals; with observations on the genera, *Asteria*, *Euryale*, *Comatula*, and *Marsupites*: Bristol, C. Frost, 150 p.

Miller, S.A., 1889, North American Geology and Paleontology: Cincinnati, Western Methodist Book Concern, 664 p.

Miller, S.A., 1890, The structure, classification, and arrangement of American Paleozoic crinoids into families: The American Geologist, v. VI, p. 275–286, p. 340–357.

Monteverde, D.H., 1992, Bedrock geologic map of the Sussex County, New Jersey portions of the Culvers Gap and Lake Maskenozha Quadrangles: Geologic Map Series 92-1, scale 1:24,000, 1 sheet.

Moore, R.C., 1978, Flexibilia, *in* Moore, R.C. and Teichert, C., eds., Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Volume 2: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. T759–T812.

Moore, R.C., and Lane, N.G., 1978, Superfamily Merocrinacea S.A. Miller, 1890, *in* Moore, R.C. and Teichert, C., eds., Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Volume 2: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. T626–T630.

Moore, R.C., and Laudon, L.R., 1943, Evolution and Classification of Paleozoic Crinoids: Geological Society of America Special Paper 46, 153 p.

Moore, R.C., Lalicker, C.G., and Fischer, A.G., 1952, Invertebrate Fossils: New York, Toronto, and London, McGraw-Hill Book Company, Inc., 766 p.

Moore, R.C., Lane, N.G., and Strimple, H.L., 1978, Suborder Dendrocrinina Bather, 1899, *in* Moore, R.C. and Teichert, C., eds., Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Volume 2: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. T606–T607.

Moore, R.C., Strimple, H.L, and Lane, N.G., 1978, Suborder Poteriocrinina Jaekel, 1918, *in* Moore, R.C. and Teichert, C., eds., Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Volume 2: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. T630.

Nelson, W.J., 1998, Bedrock geologic map of the Paducah 1°x2°Quadrangle, Illinois, Indiana, Kentucky, and Missouri: U.S. Geological Survey Bulletin 2150-B, scale 1:250,000, 1 sheet, 36 p. text.

Nicholson, H.A., and Lydekker, R., 1889, A Manual of Palaeontology: Edinburgh and London, William Blackwood and Sons, 885 p.

Ohern, D.W., 1913, Systematic paleontology of the Lower Devonian deposits of Maryland: Maryland Geological Survey Lower Devonian, p. 249–258.

Paris, F., Boumendjel, K., Morzadec, P., and Plusquellec, Y., 1997, Synthèse chronostratigraphique du Dévonien de l'Ougarta (Sahara occidental, Algérie): Annales de Société Géologique du Nord, v. 5, p. 117–121.

Parsley, R.L., and Sumrall, C.D., 2007, New recumbent echinoderm genera from the Bois D'arc Formation: Lower Devonian (Lochkovian) of Coal County, Oklahoma: Journal of Paleontology, v. 81, p. 1486–1493.

Plusquellec, Y., Boumendjel, K., Morzadec, P., and Paris, F., 1997, Les faunes Dévoniennes d'Ougarta dans la paléogéographie des régions Maghrébo-Européennes: Annales de Société Géologique du Nord, v. 5, p. 123–128.

Prokop, R.J., 1976, The genus *Edriocrinus* Hall, 1859 from the Devonian of Bohemia (Crinoidea): Casopis pro Mineralogii a Geologii, v. 21, p. 187–191.

Prokop, R.J., 1987, The stratigraphical distribution of Devonian crinoids in the Barrandian area (Czechoslovakia): Newsletters on Stratigraphy, v. 17, p. 101–107.

Prokop, R.J., 2013, *Simakocrinus* gen. nov. (Crinoidea, col.) from the Bohemian Early and Middle Devonian of the Barrandian area (Czech Republic): Acta Musei Nationalis Pragae, Series B-Historia Naturalis, v. 69, p. 65–68.

Prokop, R.J., and Petr, V., 1995a, *Edriocrinus* cf. *ata* Prokop, 1976 (Crinoidea) from the Koneprusy Limestone of the Bohemian Lower Devonian, attached inside a platyceratid shell: Casopis Narodniho Muzea, Rada Prirodovedna, v. 164, p. 105–106.

Prokop, R.J., and Petr, V., 1995b, New finds of isolated cup plates of the crinoid genus *Edriocrinus* in the Bohemian Lower and Middle Devonian: Casopis Narodniho Muzea, Rada Prirodovedna, v. 164, p. 49–50.

Prokop, R.J., and Turek, V., 2014, Thecal cup of the crinoid *Edriocrinus* preserved inside the shell of an orthocone cephalopod: Middle Devonian, (Eifelian) from Bohemia: Acta Musei Nationalis Pragae, Series B-Historia Naturalis, v. 70, p. 219–222.

Rasmussen, H.W., 1978, Suborder Holopodina, *in* Moore, R.C. and Teichert, C., eds., Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Volume 3: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. T836–T839.

Rathbun, R., 1905, Appendix II. List of accessions, 1902–3: Annual Report of the Board of Regents of the Smithsonian Institution, Showing the Operations, Expenditures, and Condition of the Institution for the Year Ending June 30, 1903. Report of the U.S. National Museum, p. 95–142.

Rickard, L.V., 1975, Correlation of the Silurian and Devonian rocks in New York state: New York State Museum and Science Service Map and Chart Series v. 24, 4 sheets, 16 p. text.

Rickard, L.V, and Zenger, D.H, 1964, Stratigraphy and paleontology of the Richfield Springs and Cooperstown Quadrangles, New York: New York State Museum and Science Service, scale 1:48,000, 2 sheets, 101 p. text.

Schlüter, C., 1878, Ueber einige astylide crinoiden: Zeitschrift der Deutschen Geologischen Gesellschaft, v. XXX, p. 28–66.

Schlüter, C., 1900, Ueber einige versteinerungen des Unter-Devon: Zeitschrift der Deutschen Geologischen Gesellschaft, v. 52, p. 178–182.

Schmidt, W.E., 1941, Die Crinoiden des Rheinischen Devons II. Teilung A. Nachtrag zu: Die Crinoiden des Hunsrückschiefers; B. Die Crinoiden des Unterdevons bis zur *cultrijugatus*-Zone (mit Ausschluß des Hunsrückschiefers): Abhandlungen der Preußischen Geologischen Landesanstalt, v. 182, 253 p.

Schuchert, C., 1905, On Siluric and Devonic Cystidea and *Camarocrinus*: Smithsonian Miscellaneous Collections, v. 47, p. 201–272.

Scotese, C.R., and McKerrow, W.S., 1990, Revised World maps and introduction, *in* McKerrow, W.S., and Scotese, C.R., eds., Palaeozoic Palaeogeography and Biogeography: The Geological Society Memoir 12, p. 1–21.

Seilacher, A., and Hauff, R.B., 2004, Constructional morphology of pelagic crinoids: Palaios, v. 19, p. 3–16.

Seilacher, A., and MacClintock, C., 2005, Crinoid anchoring strategies for soft-bottom dwelling: Palaios, v. 20, p. 224–240.

Shimer, H.W., and Shrock, R.R., 1944, Index Fossils of North America: Cambridge, The M.I.T. Press, 837 p.

Shrock, R.R., and Twenhofel, W.H., 1953, Principles of Invertebrate Paleontology: New York, Toronto, and London, McGraw-Hill Book Company, Inc., 816 p.

Simms, M.J., and Sevastopulo, G.D., 1993, The origin of articulate crinoids: Palaeontology, v. 36, p. 91–109.

Slavík, L., and Hladil, J., 2020, Early Devonian (Lockhovian–early Emsian) bioevents and conodont response in the Prague Synform (Czech Republic): Palaeogeography, Palaeoclimatology, Palaeoecology, v. 549, doi: 10.1016/j.palaeo.2019.04.004.

Smosna, R., 1988, Paleogeographic reconstruction of the Lower Devonian Helderberg Group in the Appalachian Basin, *in* McMillan, N.J, Embry, A.F., and Glass, D.J., eds., Devonian of the World: Proceedings of the Second International Symposium on the Devonian System, volume I: regional syntheses: Canadian Society of Petroleum Geologists Memoir 14, p. 265–275.

Springer, F., 1920, The Crinoidea Flexibilia: Smithsonian Institution Publication 2501, 645 p.

Stewart, G.A., 1922, The fauna of the Little Saline Limestone in Ste. Genevieve County: The Devonian of Missouri, v. XVII, p. 213–275.

Stose, G.W., and Swartz, C.K., 1912, Description of the Pawpaw and Hancock Quadrangles: U.S. Geological Survey Geologic Atlas of the United States, Folio 179.

Strimple, H.L., 1963, Crinoids of the Hunton Group (Devonian–Silurian) of Oklahoma: Oklahoma Geological Survey Bulletin, v. 100, 169 p.

Strimple, H.L., 1977, Possible commensal relationship between *Edriocrinus* and the bulbous float of *Scyphocrinites* (Crinoidea: Echinodermata): Oklahoma Geology Notes, v. 5, p.171–173.

Strimple, H.L., 1978, Family Edriocrinidae, *in* Moore, R.C. and Teichert, C., eds., Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Volume 2: Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. T812.

Swartz, C.K., 1913, Correlation of the Lower Devonian: Maryland Geological Survey Lower Devonian, p. 96–132.

Swartz, C.K., Maynard, T.P., Schuchert, C., and Rowe, R.B., 1913, Local sections of the Lower Devonian: Maryland Geological Survey Lower Devonian, p. 133–190.

Swartz, F.M., 1929a, The Helderberg Group from central Pennsylvania to southwestern Virginia: The Pennsylvania State College Mineral Industries Experiment Station Bulletin, v. 4, 28 p.

Swartz, F.M., 1929b, The Helderberg Group of parts of West Virginia and Virginia: Shorter Contributions to General Geology, U.S. Geological Survey Professional Paper 158-C, p. 27–75.

Swartz, F.M., 1939, The Keyser Limestone and Helderberg Group: The Devonian of Pennsylvania: Pennsylvania Geological Survey Bulletin, v. G 19, p. 29–91.

Swezey, C.S., 2002, Regional stratigraphy and petroleum systems of the Appalachian Basin, North America: U.S. Geological Survey Geologic Investigations Series Map I-2768, 1 sheet.

Talbot, M., 1905, Revision of the New York Helderbergian crinoids: The American Journal of Science, v. CLXX, p. 17–34.

Tansey, V.O., 1922, The fauna and the correlation of the Bailey Limestone in the Little Saline Creek area of Ste. Genevieve County, Missouri: The Devonian of Missouri, v. XVII, p. 166–212.

Ubaghs, G., 1978, Skeletal morphology of fossil crinoids, *in* Moore, R.C. and Teichert, C., eds., Treatise on Invertebrate Paleontology, Part T, Echinodermata 2, Volume 1:

Boulder, Colorado, and Lawrence, Kansas, Geological Society of America (and University of Kansas Press), p. T58–T216.

Van Sant, J.F., and Lane, N.G., 1964, Crawfordsville (Indiana) crinoid studies: The University of Kansas Paleontological Contributions, Echinodermata Article 7, v. 35, p. 1–136.

Velebilová, L., and Šarf, P., 1996, Application of microfacies analysis in the Lower Devonian of the Barrandian, central Bohemia: Journal of the Czech Geological Society, v. 41, p. 105–115.

von Zittel, K.A., 1895, Grundzüge der Palaeontologie (Palaeozoologie): München und Leipzig, R. Oldenbourg, 971 p.

Wachsmuth, C., and Springer, F., 1879, Revision of the Palaeocrinoidea: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 31, no. 3, p. 226–378.

Wachsmuth, C., and Springer, F., 1881, Revision of the Palaeocrinoidea, part II. Family Sphaeroidocrinidae, including the sub-families Platycrinidae, Rhodocrinidae, and Actinocrinidae: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 33, p. 77–414.

Wachsmuth, C., and Springer, F., 1885, Revision of the Palaeocrinoidea, part III. Discussion of the classification and relations of the brachiate crinoids, and conclusion of the generic descriptions: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 37, p. 225–364.

Wachsmuth, C., and Springer, F., 1886, Revision of the Palaeocrinoidea, part III, section II. Suborder Articulata: Proceedings of the Academy of Natural Sciences of Philadelphia, v. 38, p. 64–226.

Wanner, J., 1915. Neues über *Lodanella mira* E. Kayser: Palaeontologische Zeitschrift, v. 2, p. 81–87.

Webster, G.D., and Maples, C.G., 2008, Cladid crinoid radial facets, brachials, and arm appendages: a terminology solution for studies of lineage, classification, and paleoenvironment, *in* Ausich, W.I., and Webster, G.D., eds., Echinoderm Paleobiology: Bloomington and Indianapolis, Indiana University Press, p. 197–226.

Wehrmann, A., Hertweck, G., Brocke, R., Jansen, U., Königshof, P., Plodowski, G., Schindler, E., Wilde, V., Blieck, A., and Schultka, S., 2005, Paleoenvironment of an Early Devonian land-sea transition: a case study from the southern margin of the Old Red Continent (Mosel Valley, Germany): Palaios, v. 20, p. 101–120.

Weller, S., 1900, A preliminary report on the stratigraphic paleontology of Walpack Ridge, in Sussex County, New Jersey: Geological Survey of New Jersey Annual Report of the State Geologist for the year 1899, p. 1–46.

Weller, S., 1902, The composition, origin, and relationships of the Corniferous fauna in the Appalachian province of North America: The Journal of Geology, v. 10, p. 423–432.

Willard, B., and Cleaves A.B., 1938, A Paleozoic section in south-central Pennsylvania: Pennsylvania Geological Survey Bulletin, v. G 8, 36 p.

Wilson, C.W., Jr., 1949, Pre-Chattanooga stratigraphy in central Tennessee: State of Tennessee Department of Conservation Division of Geology Bulletin, v. 56, 415 p.

Witzke, B.J., Frest, T.J., and Strimple, H.L., 1979, Biogeography of the Silurian–Lower Devonian echinoderms, *in* Gray, J. and Boucot, A.J., eds., Historical Biogeography, Plate Tectonics, and the Changing Environment, Proceedings of the Thirty-Seventh Annual Biology Colloquium and Selected Papers: Corvallis, Oregon State University Press, p. 117–129.

Wright, D.F., 2015, Fossils, homology, and “Phylogenetic Paleo-ontogeny”: a reassessment of primary posterior plate homologies among fossil and living crinoids with insights from developmental biology: Paleobiology, v. 41, p. 570–591.

Wright, D.F., 2017, Bayesian estimation of fossil phylogenies and the evolution of early to middle Paleozoic crinoids (Echinodermata): Journal of Paleontology, v. 91, p. 799–814.

Wright, D.F., Ausich, W.I., Cole, S.R., Peter, M.E., and Rhenberg, E.C., 2017, Phylogenetic taxonomy and classification of the Crinoidea (Echinodermata): Journal of Paleontology, v. 91, p. 829–846.

Ziegler, W., 1979, Historical subdivisions of the Devonian, *in* House, M.R., Scrutton, C.T., and Bassett, M.G., eds., The Devonian System: London, The Palaeontological Association, Special Papers in Palaeontology 23, p. 23–47.

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