Phylogenetic Paleobiology: Phenotypic Diversification and Evolutionary Radiation in Paleozoic Crinoids

DISSERTATION

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By

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Abstract

Phylogenetic paleobiology is an interdisciplinary research program at the nexus of paleontology, systematics, and evolutionary biology. Specifically, phylogenetic paleobiology integrates the deep-time data, techniques, and geologic perspectives of paleontology with phylogeny-based statistical and computational approaches in macroevolutionary biology. Chapters contained within this dissertation revolve around two primary themes: (1) understanding patterns of biodiversity change over geologic time, and (2) assembling a clearer picture of the phylogeny, evolution, and geologic history of marine invertebrates, especially the Crinoidea (Echinodermata).

Under the umbrella of phylogenetic paleobiology, the primary objective of this dissertation is to help bridge the disciplinary gap between specimen-based paleontology and statistical approaches in phylogenetic comparative methods. The chapters herein use advanced statistical phylogenetic methods, such as Bayesian “tip-dating” approaches, to infer phylogenetic trees of fossil species, quantify rates of phenotypic evolution, and document patterns of morphospace occupation among fossil members of the Crinoidea (Echinodermata).

In addition to these broader studies, a major taxonomic revision of fossil and extant Crinoidea (Echinodermata) is proposed herein, as well as taxonomic description of a new genus of fossil crinoid from the Ordovician (Katian) of Ontario.
This work is jointly (and lovingly) dedicated to (1) my parents, for being supportive of my decision to pursue academic interests; (2) to my wife Lena, for her encouragement, friendship, and kindness; and (3) to my dog Gluey, for showing me how beautiful the world can be.
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Chapter 1: Overview

Introduction

A fundamental aspect of biodiversity is its tremendous propensity to vary across multiple scales and hierarchical levels. Components of biodiversity, such as morphologic diversity and taxonomic richness, vary widely among clades and through geologic time. Understanding the processes that regulate large-scale variation in Earth’s biodiversity requires integrating quantitative models of phenotypic evolution with macroevolutionary theories describing how large-scale Earth-system processes and global change events modify the structure and evolution of adaptive landscapes over geologic time.

For at least 3.5 billion years, episodes of diversification and extinction have shaped and pruned the vast evolutionary tree of life. Despite the spectacular array of Earth’s present day biodiversity, the estimated ~8.7 million species inhabiting the planet today represent a small sample of all species that have ever existed (Foote and Miller, 2007; Mora et al., 2011).

Fortunately, the fossil record provides a wealth of data regarding the morphology, spatial distribution, and temporal duration of lineages over long timescales. Although also incompletely sampled, the fossil record details the geologic history of Earth’s biodiversity and offers the only direct, empirical record of evolution’s trajectory, long-term trends, intermediate forms, and former glory of extinct clades. Thus, the fossil
record provides a natural, model system for studying macroevolution—commonly defined as either (1) evolutionary changes taking place over time scales inaccessible to direct observation or experimentation on extant species, (2) evolutionary patterns among species rather than within an ancestor-descendant lineage, or (3) any process(es) resulting in large-scale evolutionary change (Simpson, 1944; Eldredge and Gould, 1972; Stanley, 1979; Erwin, 2000; Hunt and Rabosky, 2014).

*Phylogenetic Paleobiology*

Phylogenetic paleobiology is an emerging interdisciplinary research program at the nexus of paleontology, systematics, and evolutionary biology. Specifically, phylogenetic paleobiology integrates the deep-time data, techniques, and geologic perspectives of paleontology with phylogeny-based statistical and computational approaches in macroevolutionary biology. Phylogenetic paleobiology is primarily concerned with the development and application of mathematical methods and evolutionary models to (1) estimate evolutionary relationships among lineages of extinct taxa, and (2) to study the tempo and mode of trait evolution among lineages using phylogenetic trees of fossil species (Hunt and Slater, 2016). A schematic of this research program and how it unites the major features of this dissertation is depicted in Figure 1.1.

*Crinoidea (Echinodermata)*

Echinoderms are a diverse and ecologically significant phylum of marine animals with an exceptional fossil record and are represented by more than 7,000 species in
today’s oceans. The Echinodermata includes familiar animals such as starfish, sea urchins, and sand dollars. The apparent diversity of echinoderms alive today masks their more prodigious geologic history. For example, the subclass Crinoidea (feather stars and sea lilies) comprises an evolutionary lineage of reef-dwelling to deep water echinoderms represented by ~600 species today, yet more than 8,000 fossil species have been described spanning some 480 million years of evolutionary history.

Fossil crinoids are an ideal taxon for studying trait evolution and diversification because they are a long-ranging, well-sampled taxonomic group (Foote and Raup, 1996) and preserve aspects of their feeding ecology and functional morphology as fossils (Lane, 1971; Ausich, 1980; Brower, 2007, Baumiller, 2008). Further, crinoids are highly amenable for morphology-based phylogenetic analyses because they are comprised of many discrete, homologous morphological characters (Moore and Laudon, 1943; Ausich, 1988, 1998; Foote, 1999). The combination of a well-sampled geologic history and the propensity to construct phylogenetic hypotheses makes fossil crinoids a well-suited taxon for integrating phylogenetic comparative methods with paleontological approaches to studying macroevolution (Slater and Harmon, 2013).

Summary of Contents

Using the framework of phylogenetic paleobiology and the fossil record of crinoid echinoderms, this dissertation is comprised of six semi-independent research projects concerning the phylogeny, classification, phenotypic evolution, and evolutionary radiation of Paleozoic crinoids, with emphasis placed on the Cladida.
Each chapter represents a distinct contribution proportional to a stand alone scientific paper (Figure 1.1). Indeed, the content in chapters 2-4 has either already been published (Wright, 2015) or accepted for publication in peer-reviewed scientific journals (Wright, in press; Wright et al., in press). Chapters 5-6 represent early versions of manuscripts to be submitted for publication following the defense of this dissertation. The details of these projects are described more fully below.

*Chapter 2: Fossils, homology, and “Phylogenetic Paleo-ontogeny”: a reassessment of primary posterior plate homologies among fossil and living crinoids with insights from developmental biology*

Homology is a fundamental concept in biology because it provides an evolutionary explanation for why similar features are shared by different organisms—they both inherited that feature from a common ancestor. However, the distributions of “primary” homologies among species reflect a prior belief in what constitutes comparable organismal elements and are the principal determinants of the outcome of phylogenetic analysis. Thus, it is critical that primary homology statements are well justified when conducting phylogeny-based research. This chapter combines information on fossil morphology, phylogenetic systematics, and insights from evolutionary developmental biology to reassess a set of historically contentious calyx plate homologies in non-camerate crinoids. The content of this chapter was published in *Paleobiology* (Wright, 2015).
Chapter 3: Bayesian estimation of fossil phylogenies and the evolution of early to middle Paleozoic crinoids (Echinodermata)

The application of computational methods to infer evolutionary relationships among fossil species is becoming increasingly common in paleobiological studies. However, most methods of phylogenetic inference typically used by paleontologists do not accommodate the idiosyncrasies of fossil data and therefore do not take full advantage of the information provided by the fossil record. However, recent advances in fossil “tip-dating” offer paleontologists a statistical approach to combine morphologic and stratigraphic data with probabilistic models to infer phylogenies of fossil taxa. In this chapter, I describe the basics of Bayesian tip-dating phylogenetics, describe the fossilized birth–death process model and its utility as a tree prior distribution, and present an empirical application of these techniques inferring the phylogeny of Ordovician through Devonian crinoids. The content of this chapter has been accepted for publication in the Journal of Paleontology (Wright, in press).

Chapter 4: Phylogenetic taxonomy and classification of the Crinoidea (Echinodermata)

Biological classification systems are most useful when they convey phylogenetic relationships and facilitate lucid communication among researchers. In the Linnaean system, species are arrayed into higher taxonomic ranks of increasing inclusivity based on various criteria for delimiting taxa and their ranks. Ideally, a taxon’s rank in the hierarchy provides a coarse statement of evolutionary relationships. In contrast, phylogenetic taxonomy eschews ranks and instead defines taxa based on phylogenetic
relationships alone and delineates their taxonomic content based on phylogenetic hypotheses. This chapter builds on a number of recent quantitative phylogenetic analyses and uses the principles of phylogenetic taxonomy to propose a series of stem- and node-based definitions for all major taxa (fossil and extant) traditionally recognized within the Crinoidea. In addition, a phylogeny-based revision to the traditional rank-based Linnaean classification is also proposed. The content of this chapter has been accepted for publication in the *Journal of Paleontology* (Wright et al., in press).

**Chapter 5: Ecologic innovation and phenotypic constraint in the evolutionary radiation of Paleozoic crinoids**

The application of model-based approaches to estimating evolutionary trees and the development of phylogeny-based statistical methods have greatly expanded paleobiological research programs investigating the tempo and mode of morphologic evolution. In this chapter, I test the relationships between phylogeny-based rates of morphologic evolution, taxonomic diversification, and morphospace occupation in the ~200 million year evolutionary radiation of Paleozoic crinoids. Results indicate phenotypic diversification is more complex than models commonly assumed in comparative biology, at least over geologic timescales—highlighting the need for continued synthesis between fossil and phylogenetic approaches to macroevolution. This chapter represents an early version of a manuscript currently in preparation for submission to a peer-reviewed journal.
Chapter 6: Crinoids from the Bobcaygeon and Verulam Formations (Upper Ordovician) near Brechin, Ontario: new taxa and emended descriptions

The Upper Ordovician (lower Katian) Bobcaygeon and Verulam Formations near Brechin, Ontario are comprised of a highly diverse, well-preserved crinoid fauna. This fauna provides an exceptional window into a taxonomically diverse Late Ordovician crinoid community from the interval between the Sandbian diversity peak and the end-Ordovician extinction. A survey of newly collected material from the Bobcaygeon and Verulam Formations reveals a large number of exceptionally preserved crinoid specimens with arms, stems, and attachment structures intact. Focusing on taxa placed within the Cladida, this chapter contains taxonomic descriptions for a new genus, comprised of two new species, and additional descriptions for other species within the Brechin fauna. This chapter is a nascent version of a manuscript focusing on cladid species preserved in the Brechin fauna and is part of a much broader work conducting a taxonomic re-evaluation of fossil crinoids from the Ordovician of Ontario.
References


Wright, D.F., 2015, Fossils, homology, and “Phylogenetic Paleo-ontogeny”: a reassessment of primary posterior plate homologies among fossil and living


Figure 1.1 The logical structure and interdependence of research domains within phylogenetic paleobiology. Major research areas emphasized in each chapter are depicted along with their cascading effects, where each arrow tip points toward an area that depends (in part) on information gathered within the domain located at the arrow tail. Areas of emphasis within phylogenetic paleobiology are in bold, italicized text.
Phylogenetic Paleobiology

Chapter 2
Propose homologies

Chapters 3 and 5
Infer evolutionary relationships

Chapter 4
Revise classification

Chapter 5
Macroevolutionary analysis

Chapter 6
Alpha taxonomy

Fig. 1.1
Chapter 2: Fossils, homology, and “Phylogenetic Paleo-ontogeny”: a reassessment of primary posterior plate homologies among fossil and living crinoids with insights from developmental biology

**Abstract.**—Paleobiologists must propose a priori hypotheses of homology when conducting a phylogenetic analysis of extinct taxa. The distributions of such “primary” homologies among species are fundamental to phylogeny reconstruction because they reflect a prior belief in what constitutes comparable organismal elements and are the principal determinants of the outcome of phylogenetic analysis. Problems arise when fossil morphology presents seemingly equivocal hypotheses of homology, herein referred to as antinomies. In groups where homology recognition has been elusive, such as echinoderms, these problems are commonly accompanied by the presence (and persistence) of poor descriptive terminology in taxonomic literature that confounds an understanding of characters and stymy phylogenetic research. This paper combines fossil morphology, phylogenetic systematics, and insights from evolutionary developmental biology to outline a research program in Phylogenetic Paleo-ontogeny. A “paleo”-ontogenetic approach to character analysis provides a logical basis for homology recognition and discerning patterns of character evolution in a phylogenetic context. To illustrate the utility of the paleo-ontogenetic approach, I present a reassessment of
historically contentious plate homologies for “pan-cladid” crinoids (Cladida, Flexibilia, Articulata). Developmental patterns in living crinoids were combined with the fossil record of pan-cladid morphologies to investigate primary posterior plate homologies. Results suggest the sequence of morphologic transitions unfolding during the ontogeny of extant crinoids are developmental relics of their Paleozoic precursors. Developmental genetic modules controlling posterior plate development in pan-cladid crinoids have likely experienced considerable constraint for over 250 million years and limited morphologic diversity in the complexity of calyx characters. Future phylogenetic analyses of pan-cladids are recommended to consider the presence of a single plate in the posterior region homologous with the radianal, rather than the anal X, as is commonly assumed.

Introduction

“...to avoid the taint of theory in morphology is impossible, however much it may be wished. The whole science is riddled with theory. Not a specimen can be described without the use of a terminology coloured by theory, implying the acceptance of some one or other theory of homologies.” –William Bateson (1894: p. vii)

Paleobiologists study the rich, geologic history of fossilized morphologies to examine patterns and processes in macroevolution. The ~520 million year history of
metazoan evolution revealed by fossils provides an empirical record of mass extinctions, morphologic innovations, and adaptive radiations otherwise unknowable from observations on extant species alone (Sepkoski 1981; Alroy 2010). Such studies are of interest to ecologists, developmental, and evolutionary biologists because they offer insight into evolution on timescales inaccessible to direct observation or experimentation. Integration between paleobiology and other biologic disciplines frequently leads to a better understanding of evolutionary patterns and processes at multiple hierarchical levels. For example, combining the stratigraphic record of fossil occurrences with recent discoveries in evolutionary developmental biology (EDB, or “evo-devo”) has facilitated unprecedented insights into the causal mechanisms of morphologic diversity, body plan evolution, and developmental links between micro- and macroevolution (Shubin and Marshall 2000; Raff 2007; Wagner 2007; Carroll 2008; Erwin and Davidson 2009).

Many studies combining fossils with other biologic disciplines, such as developmental biology, utilize phylogenetic information at coarse taxonomic levels (Raff 2007). Unfortunately for paleobiologists, transformations between ancestor-descendent morphologies at low taxonomic levels are not always unambiguously arrayed in stratigraphic succession. The fossil record is notoriously incomplete and can obscure patterns of first and last appearances (Smith 2001). In addition to paleontologic incompleteness, mosaic and/or heterogeneous rates of phenotypic evolution frequently confound accurate interpretations of morphologic disparity and taxonomic evolution (Erwin 2007). In an attempt to account for these difficulties, paleobiologists are increasingly using quantitative computational methods (e.g., maximum parsimony,
Bayesian inference) to construct phylogenetic hypotheses for fossil taxa rather than relying on “expert” taxonomic opinion and/or the stratigraphic distribution of first and last appearances. Reconstructed phylogenies of fossil taxa are becoming commonplace for analyzing a broad swath of macroevolutionary topics ranging from extinction dynamics (Purvis 2004; Harnik et al. 2014) to phenotypic trait evolution (Wagner 1995; Bapst 2014) and paleobiogeography (Lieberman 2001; Wright and Stigall 2014). Importantly, phylogenetic information is necessary for fossil occurrences to be meaningfully applied with other kinds of evolutionary data such as in EDB (Raff 2007).

The use of model phylogenies as a template for paleobiological studies is not without concern (Wagner 2000a). Setting aside methodological issues involving optimality criteria (Wright and Hillis 2014), the accuracy of recovered phylogenies are fundamentally limited by the information content of their underlying morphologic data and a researcher’s ability to codify fossil morphology into a set of a priori hypotheses of homology. Therefore, choosing a robust set of primary homologies (sensu de Pinna 1991) is critical to reconstructing model phylogenies. Given their importance for accurately reconstructing phylogenetic trees, how should paleobiologists propose homologous features in extinct lineages? What criteria form a logical basis for choosing among hypotheses of homologies when alternatives are possible? How are these hypotheses tested to discover features that reflect “true” evolutionary homologies?

This paper presents a combined phylogenetic and “paleo”-ontogenetic approach to these questions (cf. Mooi et al. 2005). A research program in Phylogenetic Paleo-ontogeny combines fossils, phylogenetic systematics, and evolutionary developmental
biology to provide a logical basis for discovering homologies and discerning patterns of character evolution among fossil species. As an example, I present a character analysis of posterior plate homologies among fossil and living crinoids (Echinodermata, Crinoidea) to illustrate how combining fossil morphology with developmental data can help resolve homology schemes and provide an ontogenetic basis for generating phylogenetic hypotheses of fossil taxa. The reassessment presented herein not only provides a step towards building a phylogeny that links extant crinoids with their Paleozoic ancestors but may also be useful guide for other researchers seeking a logical rationale when proposing homology statements for fossil taxa. As a prelude to my discussion on crinoid plate homologies, I first present an overview of theoretical and epistemological aspects of homology and discuss their relationship with phylogenetic systematics. Throughout, I integrate concepts from EDB when discussing homology and phylogenetic systematics to develop a general framework for a research program in Phylogenetic Paleo-ontogeny.

**Homology: conceptual basis and operational definition**

The concept of homology is fundamental to evolution and permeates all aspects of biology (Laubichler 2000). Despite its significance, homology is a seemingly elusive concept because different disciplines use the word in different ways (Brigandt 2003). For example, an evolutionary (paleo)biologist might propose an historical definition of homology involving a comparison of morphologic structures among species to reveal a
sequence of adaptive transformations. In contrast, an evolutionary developmental biologist may instead prefer a mechanistic definition where homologous features are described in terms of their underlying developmental genetics. Contrasts between perspectives are potentially problematic for relating fossilized morphologies to mechanistic definitions of homology because the overwhelming majority of species known from fossils are entirely extinct and therefore unavailable for study in an evo-devo laboratory. More worrisome for paleobiologists is the knowledge that paralogous genes may produce superficially “homologous” morphological structures, and truly homologous loci may control non-homologous structures (e.g., Bolker and Raff 1996).

In light of evolution, differing perspectives of homology (i.e., historical and mechanistic) among disciplines are united by a common theoretical basis: homology is best viewed as a concept reflecting the continuity of information in the context of phylogenetic history (van Valen 1982). Ever since Darwin (1859) the concept of homology has been used intuitively among biologists to convey the “same” features in different species arising from shared common ancestry. Recent insights from EDB suggests that the “same-ness” underlying complex morphologic structures result from the inheritance of gene regulatory networks (GRNs) with co-adapted transcription factors rather than the cumulative expression of individual “homologous” genes (Wagner 2007; Erwin and Davidson 2009). Indeed, most morphologic evolution likely results from changes in cis-regulatory elements rather changes in gene number or protein function (Carroll 2008). GRNs can be dissected into quasi-independent “developmental modules” responsible for the occurrence, reoccurrence, and modification of a morphological
character across a phylogeny (Wagner 1996; Arnone and Davidson 1997). Thus, a unified definition of homology combines developmental causality with phylogenetic continuity (Hall 2003).

The phylogenetic distribution of homologous information is hierarchically nested across multiple levels of biological organization—from genes to species (Hall 2003). The notion of “deep” homology requires a decoupling between phylogenetic, phenotypic, and genetic levels of homology. Deep homology arises when identical sets of genes are shared among phylogenetically disparate taxa despite great morphological differences between them (Shubin and Marshall 2000). For example, the last decade of research in EDB has discovered striking similarities among the gene families of analogous morphological structures (Carroll 2008; Shubin and Marshall 2000). When considering morphological traits, instances of convergence or parallelism are not homologous at the phenotypic level even if such patterns are causally linked to “deep” homologies at the genetic level (Hall 2003). Because this paper is about formulating homology statements for realized fossil morphology, it is useful herein for the concept of “homology” to refer to the subset of phylogenetic information expressed in the phenotypes of ancestor-descendent lineages while recognizing that deeper genetic homologs (or paralogs) play an important role in morphologic evolution.

The theory and practice of phylogenetic systematics unites ontological and epistemological aspects of homology by providing the concept with a set of procedures that lead to its discovery in empirical data (Wiley and Lieberman 2011). In fact, the advent of phylogenetic systematics has led many biologists to equate homology with
synapomorphy (Hennig 1966; Wiley 1975; Patterson 1982; Wheeler 2012). Any trait present in an ancestor and all of its descendants is by definition a homologous trait via continuity of descent (note that synapomorphies are synapomorphies when considered at a more inclusive level). Thus, “a homology is always a synapomorphy and a synapomorphy is always a homology” (Wheeler 2012: p. 117).

Phylogenetic systematics and the discovery of homologous characters

Knowledge of “true” evolutionary homology requires knowledge of absolute truth, which is of course nonexistent in science. Phylogenetic empiricism requires observational, a priori hypotheses of homology (Wiley and Lieberman 2011). Hypotheses of homology are repeatedly tested and ultimately either corroborated or falsified on the basis of available evidence (Hennig 1966). The “discovery” of homologous characters among fossil lineages is therefore anchored by empirical observations and best approached when multiple lines of independent evidence are considered.

Ernst Haeckel claimed to have employed the “threefold parallelisms” of Louis Agassiz to infer phylogeny: ontogenetic sequences, comparative anatomy, and the phyletic transformation of fossils in geologic succession (see Gould 1973). Although theoretical and computational aspects of modern phylogenetic methods bear little resemblance to Haeckel’s, the components of Agassiz’s parallelisms still comprise the basic character data used to propose homologous characters and build phylogenies. The
essence of Agassiz’s parallelisms can be combined with the ontological basis of homology provided by EDB and the epistemological principles of phylogenetic systematics to forge an interdisciplinary research program: Phylogenetic Paleo-ontogeny.

Characters and phylogenetic hypothesis testing—Homology statements in phylogenetics originate as character data. Any observable, heritable organismal feature is potentially a phylogenetically informative character (e.g., morphologic structures, a sequence of nucleotides, developmental traits, or behavioral data). Because morphologic characters are produced by developmental modules in the GRN, the phenotype of organisms can similarly be atomized into components of semi-autonomous “morphologic modules”; where each module has a degree of independence despite some integration with other modules (Wagner 2006). The quasi-independent nature of characters underscores a common (if not ubiquitous) assumption in mathematical phylogenetic methods: a character must operationally be expressed as an independent random variable $X$ with $N$ mutually exclusive transformational states ($X_0, X_1, X_2...X_N$) in quantitative phylogenetic analysis (Sereno 1997).

De Pinna (1991) recognized two distinct levels of homology statements that arise in phylogenetic systematics: primary and secondary homologies. A primary homology refers to a proposition that two characters are homologous (de Pinna 1991). Primary homologies are generated prior to phylogenetic analysis and therefore represent a priori hypotheses. In practice, primary homology statements for characters $X_0, X_1, X_2...X_N$ are given by the distributions of transformational states among the columns of a character by taxon matrix. Primary homology statements can be falsified as instances of homoplasy or
corroborated by others characters via phylogenetic analysis. Patterson’s (1982) suggestion to examine the degree of congruence among characters forms the most decisive test of homology for morphologic characters (de Pinna 1991). Under Hennig’s (1966) auxiliary principle, primary homologies represent inchoate hypotheses of common descent. If a primary homology passes the Patterson’s congruence test, it matures into a secondary homology (de Pinna 1991).

Quantitative phylogenetic methods form a natural test of Patterson’s (1982) notion of character congruence because they utilize the covariance structure among characters simultaneously when searching for optimal tree topologies. Once an analysis results in a tree (or set of trees), characters can be mapped onto the tree(s) to delimit monophyletic groups and discover instances of homoplasy. Congruence obtains when multiple primary homology statements corroborate one another and diagnose the same monophyletic group, viz. primary homologies become secondary homologies. However, if a primary homology statement requires independent derivations in different clades, then that primary homology has been falsified by the available evidence and cannot be considered a homology at a hierarchical level inclusive of those clades. Note that homoplasies at one phylogenetic level may be considered synapomorphies when considered at a less inclusive level. Observations of character congruence in real datasets reflect a mixture of homology and homoplasy at different phylogenetic scales (Wagner 2000b).

Of course, erroneous assumptions about characters are likely to affect the accuracy of phylogenetic inferences (Wagner 2000b). Although the proposition of
primary homology statements requires a priori assumptions about what constitutes the quality of same-ness between characters, it does not require a priori assumptions regarding inferences of actual patterns of character evolution. (Those require an independent set of assumptions involving computational and/or optimality criteria in phylogenetic analysis, not discussed here.) The accuracy of all evolutionary inferences in phylogenetic systematics is constrained by what is herein termed the phylogenetic uncertainty principle. The phylogenetic uncertainty principle simply states that the certainty of any output tree topology recovered using phylogenetic methods is fundamentally limited by the inherent uncertainty in the original choice of primary homologies. Primary homologies may be falsified during phylogenetic inference (rendering phylogenetics an empirically rigorous and testable science), but the underlying character data must be assumed a priori to comprise comparable elements in the first place. The phylogenetic uncertainty principle is an epistemological constraint imposed by the nature of historical data in biology and cannot be circumvented by mathematical or other methodological techniques, although such procedures may provide useful heuristics. The identification of comparable elements in molecular phylogenetics has benefited greatly from the advent of alignment techniques for DNA sequences, but no analogous framework currently exists for morphology. Moreover, uncertainty in phylogeny reconstruction cannot be solved by continuously adding more characters, regardless of quality, to overwhelm the noise to signal ratio and increase clade resolution, particularly in morphologic systematics (Wagner 2000b; Bapst 2012). Ideally, all “errors” discovered among primary homology statements through phylogenetic analysis arise for
biologic reasons and not from poor interpretations of morphology. Therefore, it is critical when making phylogenetic inferences that all a priori assumptions of primary homology have a logical, biologic basis supported by empirical observations via character analysis.

**Character analysis: Remane’s criteria and developmental biology—Hypotheses**

Hypotheses of primary homology arise from character analysis, not phylogenetic analysis. These hypotheses are critical to accurately reconstruct evolutionary relationships because the outcome of a phylogenetic analysis is determined by the matrix analyzed (Bryant 1989). Given their fundamental importance, assessments of primary homology should be critically evaluated and only proposed after careful analysis and argumentation. Remane (1952) outlined three principles useful for recognizing potentially homologous features among organisms: (1) similarity in position, (2) similarity in structure, and (3) the existence of transitional forms.

Criterion (1) corresponds with Geoffroy Saint-Hilaire’s (1830) “principe des connexions” and refers to similarities in the topological position of a character and its relation to other characters; whereas criterion (2) refers to an “intrinsic” similarity where two or more features match in their structural details and complexity without reference to topological position (Wiley and Lieberman 2001). For a given character, an unambiguous match between criteria (1) and (2) would support the proposition of a primary homology statement. Unfortunately, it is not always clear what constitutes a “match”. Multiple hypotheses of primary homologies can arise when evolution has transformed one structure into another and/or a character has shifted in topological position. What if the evidence supporting alternative interpretations is equivocal? Criterion (3) offers a
solution to this dilemma by incorporating information on the transitional forms of fossils and development.

Observations of the embryologic stages of development combined with the geologic succession of fossilized morphologies have long helped guide the recognition of homologous characters (von Baer 1828; Darwin 1859; Hall 2002). Homologous characters need not be similar in structure or position if it can be shown they have common genealogical origins via the existence of transitional forms exhibited in developmental patterns or the fossil record. Moreover, the existence of intermediate forms in fossils and embryos provides a temporal axis to character transformations. Gilbert and Bolker (2001) pointed out that a significant feature of embryological development is not necessarily the appearance (or disappearance) of individual transient morphologic structures, it is the temporal sequence of changes the embryo undergoes and their underlying genetic mechanisms. In other words, these temporal sequences (paleontologic or developmental) themselves can provide a logical basis for proposing primary homologies.

Conflicts between homology, terminology, and phylogenetics:

examples from the Echinodermata

“I salute the echinoderms as a noble group especially designed to puzzle the zoologist.”

–Libbie H. Hyman (1955: p. vi)
A major source of character data in systematic studies come from taxonomic
descriptions of morphology. This is particularly true in studies utilizing paleontological
data because most fossils are limited to providing only morphologic information about
extinct organisms. However, taxonomic descriptions and the terminology employed
therein do not express unbiased observations of nature. All descriptive observations,
including those in this paper, are colored by theories and expectations (Eldredge and
Gould 1972). Notably, detailed taxonomic descriptions are often entrenched in theoretical
considerations of homology and rich in predictions of character evolution.

When theories of homology and character evolution change, the terminology used
to name and/or identify a character may or may not. Obviously, problems arise in
downstream comparative analyses if the descriptive terminology used to describe a
morphologic feature does not reflect its evolutionary history. The existence (and
persistence) of a poor descriptive nomenclature in taxonomic literature obfuscates
hypotheses of primary homology when building a character matrix and results in specious
topologies when such a matrix is analyzed using phylogenetic methods. The examples
below taken from echinoderm studies demonstrate that hypotheses of primary homology
should not be taken from taxonomic literature uncritically.

Echinoderm homologies and phylogeny—Echinoderms are a phylum of marine
organisms represented by more than 7,000 living species (Brusca and Brusca 2003)
distributed among five classes: Crinoidea (sea lilies and feather stars), Ophiuroidea
(brittle stars), Asteroidea (sea stars), Echinoidea (urchins and sand dollars), and
Holothuroidea (sea cucumbers). The apparent diversity of extant echinoderms masks their more prodigious geologic history. The half-billion-year echinoderm fossil record is spectacularly complete and reveals approximately 30 clades distributed among 21 taxonomic classes spanning the entire Phanerozoic Eon (Sprinkle and Kier 1987). Moreover, the calcitic endoskeletons of fossil and living echinoderms showcase a bewildering array of disparate morphologies making them ideal for studying large-scale evolutionary patterns (Foote 1992; Sprinkle and Guensburg 1997).

Yet the phylum’s extreme morphologic disparity also presents difficulties for determining homologies between and among clades and obstructs accurate phylogenetic inferences (Paul and Smith 1984; Sumrall 1997). Research assembling a “complete” echinoderm phylogeny has been stymied for decades in part due to the lack of a unified set of morphologic terms representing homologous skeletal structures and much effort has recently been applied to the problem (Mooi et al. 1994; Mooi and David 1997; Mooi et al. 2005; David et al. 2000; Sumrall 2008, 2010; Sumrall and Waters 2012; Zamora et al. 2012; Kammer et al. 2013). For example, Sumrall and Waters (2012) examined thecal plate elements among four clades of fossil blastozoan (i.e., stalked, non-crinoid) echinoderms and discovered that homologous plates in closely related clades often had different names and that some nonhomologous plates had the same name. Egregious terminology is not limited to fossil echinoderms. Mooi and David (1997) pointed out that the five living classes also have major terminological problems that obfuscate common features across clades, such as the name applied to the various expansions of the oral ring (Hyman 1955). Thus, using the traditional names of plates to construct hypotheses of
primary homology would produce spurious topologies in phylogenetic analysis because these plates are only “homologous” in the sense that they share the same name but do not share evolutionary origins. Clearly, character analyses and revisions of morphologic terms must accompany efforts to reconstruct echinoderm phylogeny.

*Crinoids as a fractal analog of a phylum*—Difficulties determining skeletal homologies are pervasive within as well as between echinoderm clades. Within the Crinoidea, the 600 or so living species constitute a fractal analog of homology problems outlined above characteristic of the phylum and offer the opportunity for a smaller-scale case-study detailing a Phylogenetic Paleo-ontogenetic approach to discovering homology (Simms 1993; Ausich 1996). Below, I resolve contention surrounding primary homologies for posterior plates of “pan-cladid” crinoids by combining data from fossil morphology and developmental patterns in living crinoids. Although conducting a comprehensive phylogenetic analysis on pan-cladid crinoids is beyond the scope of this paper, the analysis presented here provides a logical basis for choosing hypotheses of primary homologies for posterior plate characters in future phylogenetic analyses. Moreover, it is hoped that the argumentation used herein will serve as general framework for others seeking a logical basis for proposing primary homologies to test phylogenetic hypotheses.
Terminological antinomies and transitional homologies: parallels between crinoid ontogeny and fossilized evolutionary history

“The mystery of this controversy is curiously full of misunderstandings and misrepresentations.” –Bather (1891: p. 480)

Natural history of the pan-cladid Crinoidea—The Pan-Cladida are a long-lived clade of crinoids spanning the Ordovician Period (~ 485.4 Ma to 443.4 Ma) (Cohen et al. 2013) to the present and include all extant species of Crinoidea as well as fossil forms. Together, the pan-cladids are the most diverse clade of crinoids and comprise three of the five named subclasses: Cladida, Flexibilia, and Articulata (Ausich et al. in press; Wright and Ausich in press). The subclass Cladida is paraphyletic and gave rise to both the Flexibilia and Articulata (Springer 1920; Simms and Sevastopulo 1993). Thus, the name “Pan-Cladida” used herein refers to the common ancestor of all species included within the subclass Cladida and all of its descendants, regardless of taxonomic rank in the Linnaean hierarchy (Wright and Ausich in press). The flexible crinoids split from the cladids during the Late Ordovician, diversified, and went extinct at the end of the Paleozoic Era. The Articulata, of which all living crinoid species are grouped, originated from cladid ancestors either during the Late Paleozoic or earliest post-Paleozoic (Simms and Sevastopulo 1993; Webster and Jell 1999) (Fig. 2.1). Recent phylogenies of living crinoids indicate a monophyletic Crinoidea, but the monophyly of Articulata has been questioned and awaits further analysis (Rouse et al. 2013; Roux et al. 2013). Because the
greatest diversity of pan-cladid crinoids are known only as fossils, tracing the ancestry of living crinoids and discovering their phylogenetic affinities with extinct fossil lineages requires a detailed understanding of crinoid comparative morphology to generate hypotheses of homology.

The skeletal morphology of a crinoid is highly complex and consists of several morphologic modules: the size and shape of the calyx, number and arrangement of posterior plates, arm morphology and branching pattern, and stem (Fig. 2.2). The combinatorial nature of module configurations has given rise to a staggering diversity of pan-cladid morphologies and nearly 1,000 named genera. In Paleozoic cladids, the pentaradial symmetry of the calyx is interrupted by one to three plates located in the posterior CD interray of the cup. These additional, so-called “anal” (sensu Ubaghs 1978) plates, in the posterior region are referred as the radianal, anal X, and right tube plate (listed from the aboral to oral direction) (Fig. 2.2 B-C). Fossil forms display temporal variation in the number, shape, and positional relations of posterior plates (Moore et al. 1978; Webster and Maples 2006). In extant crinoids, a posterior plate is present in juvenile stages but absent in adults (Clark 1915; Amemiya et al. 2014). Because posterior plating patterns are an important module of morphologic differentiation, they have been extensively used as taxonomically significant characters for delimiting crinoid species and higher taxa (Moore et al., 1978; Webster and Maples 2006). Thus, previous attempts at testing phylogenetic hypotheses and evolutionary patterns among pan-cladids included posterior plate characters despite substantial uncertainty underlying their primary
homology statements ( Brower 1995; Ausich 1998; Gahn and Kammer 2002; Kammer 2008).

Posterior plates: temporal trends and contentious homologies—Patterns of posterior plate evolution in fossil pan-cladids have been characterized as exhibiting a “progressive change toward increased simplicity” (Moore and Laudon 1943: p. 34). The oldest known pan-cladids have multi-plated posterior interrays (Sprinkle and Wahlman 1994; Guensburg and Sprinkle 2009) and many lineages subsequently exhibit a general trend to reduce the number of posterior plates in the cup throughout the Paleozoic (Moore and Teichert 1978). Temporal changes in the number of posterior plates broadly correspond with concomitant shifts in ecologic abundance and taxonomic diversity (Webster and Maples 2006). Complex, multi-plated morphologies were the most diverse during the Ordovician and subsequently disappear from the fossil record; whereas crinoids with three posterior plates were most dominant throughout the Silurian to Pennsylvanian (Webster and Maples 2006). Crinoids with a single posterior plate rapidly diversified during the Pennsylvanian and increased in frequency to become the most common morphology during the Permian (Webster and Maples 2006). Older taxonomic literature capture these so-called progressive changes by describing a plate arrangement as having either a “primitive” or “advanced” condition, where primitive refers to stratigraphically older multi-plated morphologies and advanced refers to younger two or single-plated forms (Moore et al. 1978).

Homology schemes for posterior plates among fossil lineages and between fossil and living crinoids have been debated, somewhat inimically, for more than a century (P.
H. Carpenter 1882; Wachsmuth and Springer 1879; Bather 1980; 1891; 1918; Clark 1915; Mortensen 1920; Springer 1920; Ubaghs 1953; Moore 1962; Phillip 1964; Moore and Teichert 1978; Webster and Maples 2006). The overwhelming majority of named fossil genera have three posterior plates in the cup, including putative Paleozoic ancestors of living crinoids and fossil flexibles (Webster and Jell 1999; Webster and Maples 2006). Using Remane’s (1) criterion described above, proposing primary plate homologies for crinoids with three posterior plates is straightforward. The radianal is the most proximal posterior plate to (and always in contact with) the C radial, typically occupying a position beneath or to the left of the C radial. The anal X is interradial in position and may be in lateral contact with the radianal, C radial, BC and CD basals, or the CD basal, and occupies a position above and/or to the left of the radianal (Ubaghs 1978). The right-tube plate rests either above the radianal or both the radianal and anal X and typically provides support for other plates in the anal sac (Fig. 2.2). Where only two plates are present in the cup, Remane’s (1) criterion can once again be used to propose primary homologies for the two remaining more proximal plates: the radianal and anal X (Moore and Teichert 1978). However, any further reduction in the number of posterior plates renders Remane’s (1) criterion inapplicable because the single posterior plate does not occupy a position more similar to either the radianal or anal X where two or more posterior plates are present. In other words, one of the posterior plates migrated from its ancestral position and the other is absent.

An antinomy can be characterized as a kind of paradox that describes two equally compelling but mutually incompatible explanations and is a useful term to describe the
contention that arises when only a single posterior plate is in the cup. Choosing whether a single plate in the posterior interradius is the radianal or anal X presents an antinomy of alternative homology schemes (Fig. 2.3). If there is only one posterior plate in a fossil pan-cladid, is it the radianal or anal X? Is this fossilized single posterior plate homologous with the single plate present in the juvenile stages of extant crinoids? If so, which posterior plate is it? Unfortunately, Remane’s (2) criterion cannot help because the shape of a single posterior plate is constrained to accommodate changes in the size and shape of the calyx and therefore does not retain the shape of either the radianal or anal X when alone in the cup.

The problem is further confounded by a history of problematic terminology favoring plate topologies over plate homologies. Remarkably, a perusal of the taxonomic literature of fossil crinoids reveals the presence of a single posterior plate in a fossil cladid is frequently termed an anal X in taxonomic descriptions and figured specimens even when an author considered the plate homologous to the ancestral radianal or the evidence equivocal (cf. Moore and Laudon 1943; Ubaghs 1953; 1978; Moore 1962; Philip 1964). Kirk’s (1944: p. 234) description of the single posterior plate in the Mississippian genus Cymbiocrinus epitomizes this dubious practice: “it is doubtful if this plate is homologous to [the] anal X, but we may so denominate it for convenience”. These misnomers obfuscate any notion of evolutionary continuity among characters. It is not surprising there has been much confusion given that different sections of the crinoid Treatise of Invertebrate Paleontology (Moore and Teichert 1978) disagree with one another with respect to posterior plate homologies and terms for fossil and living pan-
cladids (cf. Breimer 1978, Brower 1978, Moore et al. 1978; Strimple 1978; and Ubaghs 1978). Thus, crinoid paleobiologists should not take Treatise descriptions of posterior plate characters at face value when proposing primary homologies to make phylogenetic inferences.

Potentially more confusing for a phylogeneticist is the terminological scheme proposed by Webster and Maples (2006). In an attempt to rectify terminological misnomers, Webster and Maples (2006) proposed to abolish all implications of homology from morphologic nomenclature by renaming the posterior plates the primanal, secundanal, and tertanal. Under this terminology, the primanal is always the most proximal plate in the cup, regardless of whether it is the radianal or anal X. Thus, Webster and Maples (2006) “solved” the epistemological dilemma of proposing homology statements by avoiding them altogether. This so-called solution is problematic for two reasons. First, because the terminology of Webster and Maples (2006) is based purely on topology without reference to any ontological theory of homology, it is useless for proposing primary homologies to test phylogenetic hypotheses. Second, the proposed terms are already in use to describe an unrelated, non-homologous set of plates in a phylogenetically distant clade of crinoids, the subclass Camerata (Moore and Teichert 1978; Ausich 1998). For these reasons, Webster and Maples’ (2006) terminology should not be followed. Instead, we should confront the problem directly by seeking a logical basis for choosing between alternative primary homology schemes. This approach has the advantage of combining posterior plate characters with other modular complexes of crinoid morphology in a phylogenetic analysis. Thus, characters can be tested against one
another when inferring phylogenetic relationships and any parallel instances of plate reduction (or addition) can be determined empirically.

In the next two sections, I apply Remane’s (3) criterion to examine potential transitional forms in two independent sources of data: the ontogeny of extant crinoids and paleontologic studies on individual lineages. The recognition of intermediate morphologies present in developmental patterns of extant representatives and/or high-resolution paleontologic sequences may provide paleo-ontogenetic evidence supporting one set of primary homologies over another and dissolve antinomies arising from examining comparative morphology alone.

Developmental patterns in living crinoids—Numerous observations of embryologic stages in extant crinoids have been described, particularly for the stalkless comatulid crinoids (Thomson, 1865; Carpenter 1866; Clark 1915; Springer 1920; Mortensen 1920; Mladenov and Chia 1983; Lahaye and Jangoux 1987; Shibata et al. 2008). Developmental patterns in living species of stalked crinoids were largely unknown until recently (Nakano et al. 2003; Amemiya et al. 2014). Because stalked crinoids and comatulids share many similarities with respect to the skeletal development of the calyx and posterior plates, the distinction between the two adult forms is not pertinent for the purposes of this paper.

Kammer (2008) lucidly described common themes of crinoid development, from which I base the following conspectus. Crinoid ontogeny consists of five successive life stages: the embryo, doliolaria, cystidean, pentacrinoid, and (in comatulids) the comatulid stage (Mladenov and Chia 1983; Lahaye and Jangoux 1987). The doliolaria is an
endotrophic, free-swimming larva that emerges from the embryonic membrane. Once the doliolaria settles on a suitable substrate, it metamorphoses into the stalked cystidean stage. The skeleton of a cystidean stage consists of paired, interradially-oriented basals and primary peristomial cover plates (i.e., oral plates, see Kammer et al. 2013), a terminal stem plate, and a few columnals. Infrabasal plates, common in fossil pan-cladids, do not usually develop in living articulates but are known to occur in some species (Rasmussen 1978). Next, more skeletal plates are added including an “anal” plate, radials, and numerous additional plates relating to the construction of the arms and pinnules initiating the exotrophic pentacrinoid stage. Comatulids become adults when they excise the stem; whereas stalked crinoids grow into larger “adult” pentacrinoids. Although variation in the details of crinoid ontogeny exists, all crinoid species exhibit the general growth sequence and patterns of skeletal plate addition outlined above.

This single posterior plate was originally called an “anal” plate in living species because it was first discovered in the pentacrinoid stage of comatulids to directly overlie the BC basal between the radials, and therefore assumed on the basis of topological position to be homologous with the anal X in fossil crinoids (Thomson 1865; Carpenter 1866; Bather 1890). However, development is not a static process and characters cannot be accurately traced by giving special consideration to a single ontogenetic stage. Skeletal plates within the calyx grow at different rates and change in size and shape over the course of ontogeny (Lahaye and Jangoux 1987). In addition, the topological arrangement of plates may vary in different growth stages. These changes must be accounted for when tracing parallels between development and evolution. Comparisons
between a single ontogenetic stage and adult morphology can lead to specious proposals of primary homology because the developmental origin of a character may not correspond to its position during a later time in ontogeny. Instead, the entire sequence of changes must be considered when connecting the developmental origin of a morphologic character with its ontogenetic history and ultimate fate in the adult.

The developmental origin, migration, and eventual resorption of the single posterior plate in juvenile crinoids have been well characterized throughout the succession of ontogenetic stages by Clark (1915), Springer (1920), and Lahaye and Jangoux (1987) (Fig. 2.4). Detailed observations by these authors demonstrate that the development of the posterior “anal” plate originates in a radial position (with respect to the basals and primary peristomial cover plates) prior to the radials during the cystidean stage, and occurs within the same radius as the C radial. When the radial plates begin to grow, the larger posterior plate occupies a position beneath and to the left of the C radial, maintaining a close affinity with the developing gut tract (Springer 1920). As the radials grow larger, the posterior plate occupies a position on the right-hand side of the CD interray and is accommodated within a concavity in the C radial plate. Eventually the radials push the posterior plate into an inter-radial position (i.e., the CD interray) where it supports a lappet that protects the developing anal cone (Lahaye and Jangoux 1987). The posterior plate subsequently migrates out of the cup and is resorbed once the anal cone has formed. In summary, the posterior plate originates in a radial position, maintains lateral continuity with the C radial, and later moves into the CD interray and out of the cup. In fossil pan-cladids with multiple posterior plates, it is the radianal that has
affinities with the C radial and maintains lateral contact with it; whereas the anal X is an interradial plate (Ubaghs 1978). Thus, the evidence from crinoid ontogeny indicates that the single, prominent posterior plate found in living crinoids is homologous with the radianal in fossil pan-cladids, not the anal X.

If the single posterior plate in the juvenile stages of living species is the radianal, is there any ontogenetic evidence for the existence of an anal X? Recall that the anal X is an interradial plate within the CD interray. Interradial plates are known to occur in several species of living comatulids and appear late in development during the pentacrinoid stage (Clark 1915; Breimer 1978). They either occur in all five interrays with the same degree of development or they are absent entirely (Breimer 1978). The early-mid pentacrinoid stage of Comactinia meridionalis displays posterior plating strikingly similar to the arrangement in many fossil cladid and flexible species, with the radianal side by side with the additional posterior plate (Springer 1920, plate B, fig. 5a). Later, the interradials are resorbed along with the radianal leading to their absence in the adult phenotype (Springer 1920; Breimer 1978). If the posterior interradial is homologous with the anal X in fossil crinoids, than the right tube plate (and any other posterior plates) in fossil pan-cladids may have developed from additional posterior interray plates. In this scenario, the interradial plates outside the CD interray either did not develop or were resorbed prior to adulthood, as they are unknown in fossil species. Alternatively, the posterior interradial plate may not be homologous with the anal X. The insertion of interradial plates may instead be a novel feature present among a subset of living comatulids. Interradial plates are presently unknown in juvenile stalked crinoids, but this
may simply reflect the paucity of developmental studies on stalked crinoids (Amemiya et al. 2014).

These observations have significant implications for ascertaining evidence-based primary homology statements if one is willing to assume geology’s useful aphorism regarding the present as the key to the past: the morphologic transitions unfolding during crinoid ontogeny are developmental relics of their Paleozoic precursors. The migration pathway of the radianal during crinoid development (viz, originating radially in the C ray followed by movement to the posterior interradius and out of the cup) parallels temporal trends in the paleontologic succession of posterior plate morphologies (Fig. 2.4). Therefore, a uniformitarian perspective supports the hypothesis that the radianal plate, not the anal X, is homologous with the single posterior plate in Paleozoic pan-cladids. Thus, the single posterior plate in the cup of a fossil pan-cladid should be coded as a primary homolog of the radianal plate occurring in crinoids with multi-plated posterior interrays. The implications of this hypothesis are not conditional on the monophyly of the Articulata because the pageant of ancestral morphologies echoed in crinoid development empirically demonstrates that the single posterior plate in at least one lineage is equivalent to the radianal, not the anal X. Given the similarities in posterior plate development among extant crinoids, a polyphyletic Articulata would only strengthen the argument above because it would suggest that the same pattern occurred independently among multiple Paleozoic ancestors.

Phyletic evolution in Paleozoic pan-cladids: a test of relative frequencies—The argumentation above concerning posterior plate homologies rests upon the assumption
that patterns of character change exhibited by extant crinoids can be extended to apply to all pan-cladid lineages known only as fossils. When conducting a phylogenetic analysis incorporating extinct pan-cladid lineages, is such an extrapolation from living representatives justified? Large-scale temporal trends in evolution need not be invariant among lineages and do not necessarily correspond to phylogenetic trends. Individual clades may exhibit idiosyncratic trends to reduce (and/or subsequently add) posterior plates iteratively over time. Nevertheless, character coding decisions must be made if one seeks to conduct a phylogenetic analysis. Moreover, the question is not whether or not extant crinoids are closely related to Paleozoic pan-cladids. All evidence indicates they are closely related and share an overlapping distribution of taxonomically significant traits (Moore and Teichert 1978; Roux et al. 2013). In the absence of any additional information, basing primary homologies on ontogenetic sequence data present in living representatives is justified because empirical science must proceed in the direction of available evidence. However, one is faced with a seemingly impossible problem of assessing how often such a hypothesis is objectively accurate.

Null hypotheses in phylogenetics are constructed by making a priori assumptions of homology among comparable characters and using Hennig’s (1966) auxiliary principle. What if a mistake is made in determining what constitutes a “comparable character” (or character state) in the first place? In other words, if the presence of a single posterior plate is determined to be equivalent to a radianal in pan-cladids during character analysis ($H_0 = \text{a single posterior plates is homologous with the radianal}$), how often has a researcher committed a type 2 error? Although such mistakes may, in principle, be
unknowable; it is humbling to consider that a type 2 error during character analysis may result in type 1 errors during phylogenetic analysis and obstruct the recognition of “true” (i.e., empirical) evolutionary homologies and patterns of character evolution.

Central tendencies in historical science must be determined by examining relative frequencies (Gould 1989). Although single or isolated occurrences of a phenomenon may be interesting and/or otherwise worthy of study, they do not provide insight into building general expectations of a theory. Luckily, the pan-cladid fossil record supplies several key examples relevant to assessing the relative frequency in which the fossil record supports or refutes available evidence from ontogeny. If examples of morphologic transitions from the fossil record predominantly corroborate the ontogeny-based solution to the posterior plate antinomy, then one can be more confident in the results of a phylogenetic analysis assuming those primary homologies to reconstruct evolutionary relationships and patterns of character evolution.

Although the fossil record of crinoid genera is well-sampled (Foote and Raup 1996), many pan-cladid species are based on only one or a few specimens (Webster and Maples 2006). All macroevolutionary studies must consider the species-level, even when using higher taxa as proxies, because species are the fundamental units that preserve phenotypic change among populations (Hendricks et al. 2014). Unfortunately, there is a dearth of pan-cladid species-level phylogenies available (Kammer and Ausich 2007; Gahn and Kammer 2012), and none contain a set of species relevant to the problem addressed here. Moreover, conducting such a species-level analysis itself may require addressing the antinomies this paper is attempting to resolve: is the single posterior plate
homologous with the radianal or anal X? A comparison of fossilized ontogenetic sequences among pan-cladids might be helpful, but there are currently no known fossils preserving the larval and early developmental stages of posterior plates. At this point, an interesting light may be thrown on the problem by examining variations in posterior plate conditions among species with transitional morphologies. The collection of a large number of specimens allows one to examine a distribution of transitional morphologies and make comparisons combining all three of Remane’s (1952) criteria.

Webster and Maples (2006) noted numerous instances where intraspecific variations in posterior plate conditions occur when a large number of specimens were collected. These examples are particularly informative because they come from paleontologically well-sampled stratigraphic sections representing short time intervals (Webster and Maples 2006). Thus, it is likely they represent paleontologic sampling taking place over short enough time scales to sample transitional morphologies. Any bed-scale time averaging and/or taphonomic discrepancies among first and last appearances between stratigraphic sections do not affect the inferences obtained herein because it is the overall distribution of sampled morphologies, not their sampled paleontologic sequence, that are used to make comparisons and examine intermediate forms.

For example, Wanner (1916) recognized the presence of a single, large interradial posterior plate in his original description of the Permian pan-cladid *Hydreionocrinus variabilis* (= *Cadocrinus variabilis*), but called this plate the radianal rather than anal X because in some specimens the position of the plate was lying at an angle to the CD basal and in a more proximal position with the C radial. Wanner (1916) noted that among the
197 specimens in his collection, a subset possessed proximal tips of one to two small plates above the radial summit, which he termed the anal X and right tube plate. Thus, Wanner (1916) concluded that the large posterior plate must actually be a large radianal that migrated to an interradial position, supporting the anal X and right tube plate above. Webster and Maples (2006) suggested that if Wanner had a smaller sample size typical of fossil pan-cladid species, he would likely have committed a misnomer by calling it an anal X. Given the inconsistent treatment in the Treatise and the standard portrayal of posterior plates in crinoid plate diagrams (Moore and Teichert 1978), it is probable that any crinoid worker since the 1800s would have nearly committed the same misnomer.

Similarly, Wright (1920; 1926; 1927) examined posterior plate conditions in a large number of Upper Paleozoic specimens of Eupachycrinus calyx (n = 1,000), Zeacrinus? konincki (n = 342), Ulocrinus globosus (n = 480), and Hydreionocrinus sp. (n = 130) (= Phanocrinus calyx, Parazeacrinites konicki, and Ureocrinus globosus respectively). Wright (1926, p. 149) noted that “extreme” variations in posterior plates are apparent in these species when samples become sufficiently large. With such a large sample size displaying a semi-continuous distribution of intermediate posterior plate conditions, Wright (1920; 1926; 1927) applied the logic of Remane’s criteria to the distribution of transitional morphologies. In all cases, the radianal can be seen to have increased in size and subsequently moved into an interradial position, pushing the other posterior plates out of the cup (e.g., Wright 1926, figs. 1-59). Intermediate morphologies display small remnants of an anal X and right tube plate above the interradially positioned radianal plate. Thus, the paleontologic evidence indicates that the posterior
plate most proximal to the C ray is the last to migrate from the cup in a phyletic sequence. Another example supporting the conclusions of Wanner (1916) and Wright (1926) was discovered by Webster and Lane (1967) for *Arroyocrinus popenoei* (n = 83).

The examples above should not be interpreted as suggesting that all (or most) species of pan-cladids exhibit variation in posterior plate position and arrangement when large samples are collected. Webster and Lane (1967) also examined *Moapacrinus rotundus* (n = 137) and *Erisocrinus longwelli* (n = 59) and found no variation in the posterior plating in either species, therefore supporting the conclusion that the above examples represent special cases where an exceptionally abundant number of specimens in an evolving lineage were sampled over a short temporal duration. Further work is needed to address whether any of the observed posterior plate variations corresponded with other characters and/or were related to speciation.

Webster and Maples (2006) compiled a reference list for the number and arrangement of posterior plates for the type species of 378 pan-cladid genera from which relative frequency of the radianal as the single posterior plate may be inferred. Their dataset includes 152 genera with three posterior plates and therefore can be unambiguously homologized between species using procedures outlined earlier in this paper. Of these, 96% have the radianal “moderately or mostly underlying the right side” of the anal X (Webster and Maples 2006: p. 200). This condition was also found to be the most common arrangement for pan-cladids with two plates in the posterior interray (Webster and Maples 2006). These paleontological observations support the hypothesis that the single posterior plate in fossil pan-cladids is predominantly the radianal, not the
anal X. Therefore, the relative frequency of morphologic transitions recovered from the fossil record overwhelmingly (≥ 96%) agrees with and corroborates the ontogenetic evidence provided by extant crinoids. This discovery is significant because it overturns more than 120 years of the status quo in crinoid paleontology.

Of course, it is possible that a small number of lineages with no living representatives lost the radianal plate yet retained the anal X. Both Kammer and Ausich (1996) and Webster and Maples (2006) suggested that this may have happened among species of the Mississippian genus *Barycrinus*. Some species of *Barycrinus* possess small radianal plates below and to the right of the much larger anal X, where others have only a single, large visible plate interpreted as an anal X. However, as noted by Gahn and Kammer (2002), it is possible that the anal X has overgrown the radianal in these species and is lamentably invisible on the calyx exterior. Although this condition is presently unknown in *Barycrinus*, it is known to occur among other Late Paleozoic pan-cladids. For example, the Pennsylvanian pan-cladid *Perimestocrinus calyculus* (= *Vertigocrinus calyculus*) described by Moore and Plummer (1940) has only two plates visible on the exterior surface of the calyx. However, three posterior plates are visible when examined from inside of the cup. When viewed from the inside of the calyx, these plates are readily interpreted as the radianal, anal X, and right tube plate occupying an otherwise ordinary arrangement (Moore and Plummer 1940). Without examining the calyx interior, one may have inferred from topology that the radianal was absent and/or incorrectly coded the exterior plates in a character matrix. Additional taxa with cryptic plates within the calyx interior include species placed in the Pennsylvanian crinoid genera *Arkarcrinus*,
Paradelocrinus, Plaxocrinus, Vertigocrinus, and the Mississippian to Permian genus Erisocrinus (Strimple, 1978; Webster and Maples 2006). Based on these considerations, further collection, preparation, and careful inspection of aberrant fossil specimens is necessary to better understand morphologies that fall outside of general expectations (see Rozhnov and Mirantsev 2014).

Crinoid ontogeny and phylogeny: implications for evolutionary studies

“Ontogeny does not recapitulate phylogeny: it creates it” — Walter Garstang (1921: p. 82)

The existence of parallels between ontogeny and phylogeny is one of the most pervasive and influential concepts in evolutionary biology and relate directly to the discovery of homologous characters (Gould 1977). Evolutionary developmental biology (EDB) has recently refurbished von Baer’s law to study parallels between evolution and development (Abzhanov 2013). Von Baer’s law states that more generalized characters appear earlier in ontogeny than specialized characters, with specialized characters developing from generalized characters (Gould 1977). For example, ontogenetic sequences for species within a clade may share generalized developmental features, but subclades may share additional more specialized features that reflect more recent evolutionary changes not shared with other subclades. Because developmental programs in the gene regulatory network (GRN) have phylogenetic memory, they retain aspects of
phylogenetic history and may “recapitulate” sensu von Baer 1828 (non Haeckel 1866) ancestral morphologies in the juvenile forms of descendants (Abzhanov 2013). Parallels between evolution and development predict a significant degree of recapitulation between cladistically significant traits nested at different phylogenetic levels (Abzhanov 2013).

Kammer (2008) suggested that the appearance and position of plates during crinoid development are likely controlled by genetic switches, such as *Hox* genes, that regulate proximal-distal morphogenesis and other aspects of skeletal development. Although developmental genetic studies on living crinoids have discovered the expression of *Hox* genes in the earliest developmental stages of the sea lily *Metacrinus rotundus* (Hara et al. 2006), it is for the moment an understatement to suggest that much work needs to be done to discover how these genes interact with other aspects of the GRN (such as *cis*-regulatory elements) to direct downstream development and morphogenesis in crinoids. Nevertheless, the near uniform predictability in the developmental timing of skeletal elements among extant comatulid and stalked species suggests they are controlled by highly conserved developmental modules.

Such evo-devo perspectives serve to strengthen the paleo-ontogenetic character analysis above. In living crinoids, the radianal appears much earlier in ontogeny than other additional plates in the posterior interray (i.e., as in *Comactinia meridionalis*) and exhibits the same degree of developmental canalization as other calyx plates (Lahaye and Jangoux 1987). Parallels between crinoid development and fossilized morphology, as interpreted using von Baer’s refurbished law in EDB, indicate that living crinoids recapitulate the morphologies of Paleozoic ancestors because they inherited a common
pathway of development (Abzhanov 2013). Thus, the regulatory machinery in the GRN controlling posterior plate development may not have substantively changed since the Late Paleozoic. This result corroborates studies by Foote (1995; 1999) examining morphologic disparity in Paleozoic and post-Paleozoic crinoids. Foote (1995) found that pan-cladids steadily increase in disparity throughout the Paleozoic despite considerable volatility in generic richness. However, pan-cladid disparity dropped after the end-Permian extinction and post-Paleozoic forms do not broadly overlap with their Paleozoic representatives in morphospace (Foote 1999). Differences in both overall disparity and morphospace occupation led Foote (1999) to conclude that genetic and/or developmental constraints may have been responsible for substantive differences between Paleozoic and post-Paleozoic crinoids. Given that posterior plate characters show considerable variation throughout the Paleozoic and are correlated with other evolutionary changes occurring in the size and shape of the calyx (Moore et al. 1978; Webster and Maples 2006), it is likely that developmental modules within the GRN of the lineage(s) that survived the end-Permian extinction became rigidly constrained. Such constraints would limit developmental variation in calyx design and decrease the propensity for lineages to expand into unoccupied regions of crinoid morphospace.

The notion of deep homology provides a potential explanation for putative parallel (i.e., homoplasious) trends in posterior plate characters occurring in different lineages of Late Paleozoic cladids (Moore et al. 1978; Webster and Maples 2006). Given the numerous paleontologic species that display a net reduction in the number of posterior plates, it is possible that different lineages lost posterior plates independently
through instances of parallel evolution. Parallel morphologic evolution can occur among distantly related lineages arising from selection acting on variation within shared developmental toolkits (Hall 2003). Because most Paleozoic pan-cladids have three posterior plates, the tendency to evolve less complex morphologies via plate reduction is interpreted as a paedomorphic trend reflecting arrested development or progenesis (Kammer 2008). Precocious maturation can result from an adaptive response to pressures for small body size and/or as an r selection strategy for rapid growth rates for taxa inhabiting unstable environments (Gould 1977). All putative ancestors of extant crinoids are members of the Late Paleozoic Crinoid Macroevolutionary Fauna (LPCMF) and broadly overlap in niche space (Kammer and Ausich 1987; Ausich et al. 1994). The transition to a cladid-dominated LPCMF was concomitant with considerable environmental changes, such as an increase in the abundance and distribution of siliciclastic habitats (relative to carbonate platforms) preferred by Late Paleozoic cladids (Kammer and Ausich 2006). This increase in siliciclastic environments is related to orogenic activity and an increase in the frequency of sediment disturbance (Walker et al. 2002). Kammer (2008) noted that pan-cladids in unstable environments commonly have smaller body sizes. Thus, decreased environmental stability in substrate conditions may have led to an increase in frequency of pan-cladids with rapid growth rates and small body sizes exhibiting paedomorphic morphologies. Given that Late Paleozoic pan-cladids likely shared many developmental modules at “deep” genetic levels, different species facing similar selection pressures may have independently evolved paedomorphic morphologies as a response to similar environmental changes. Such selection could arise
either through adaptive evolution within populations or at the species level if posterior plate characters are strongly correlated with diversification rates (Rabosky and McCune 2010). Thus, a combination of selective trends and developmental constraints are hypothesized herein to have produced parallel evolution of paedomorphic morphologies in different lineages of Late Paleozoic pan-cladids. Further exploration of these observations await the construction of model phylogenies to test the relationship between the evolutionary acquisition and environmental context of paedomorphic morphologies in Late Paleozoic pan-cladid crinoids.

The discussion above suggests homoplasy may be common for posterior plate characters in pan-cladid crinoids. An a priori belief of homoplasy is not grounds for excluding posterior plate characters from future phylogenetic analyses because not all instances of homoplasy are artifactual results of poor character state interpretations (Wagner 2000b). Character reversals and instances of parallel evolution are real events in life’s history and must be mapped onto a model phylogeny to gain insight into historical patterns of character evolution. Moreover, numerous other morphologic characters are correlated with changes in posterior plates including the presence of muscular articulations, zyzygial sutures, structure and branching of the arms, and the development of pinnules (Kammer 2008; Webster and Maples 2008). Moreover, if one were to a priori disregard from phylogenetic analysis any character with the propensity for homoplasy, there would be no characters left to study or much point to conduct a quantitative phylogenetic analysis because such a proposal assumes one already knows the “true” phylogeny and is merely cutting out “noise” among characters to generate a
more well-resolved and/or well-supported tree. To be clear, I am not advocating that homoplasious characters are desirable in phylogenetic analysis. I am only advocating that features revealed to be comparable elements through paleo-ontogenetic character analysis, as described in this paper, constitute ‘real’, empirical data that need to be rigorously tested against other characters in a phylogenetic context. Given the finite set of morphologic characters available and the important role of posterior plate characters in pan-cladid morphology, I suggest researchers employ a limited “prior belief” in the available paleo-ontogenetic evidence and therefore propose that future phylogenetic analyses consider the single posterior plate in fossil pan-cladids as a primary homolog with the radianal in multi-plated taxa.

Phylogenetic Paleo-Ontogeny: a multidisciplinary approach to discovering homology

Paleobiology, phylogenetic systematics, and EDB play complementary roles in evolutionary biology because they provide the theoretical basis and basic historical data for understanding patterns and processes of macroevolution. Phylogenetic Paleo-ontogeny constitutes a total evidence approach to homology recognition by unifying these seemingly disparate fields to propose, test, and empirically “discover” homologous characters in fossil taxa. A case study in homologizing posterior plates among pan-cladid crinoids was presented to illustrate how a research program in Phylogenetic Paleo-ontogeny can provide insight into how developmental and fossil data can be combined to
dissolve morphologic antinomies and ameliorate terminological difficulties obstructing clarity in homology schemes. It is hoped that this paper will serve as a template for other researchers seeking an ontological basis and epistemological framework for discovering homologies of fossil and living species.

For example, within the Echinodermata two models of character analysis have been proposed to resolve homologies among classes: Extraxial-Axial theory (EAT) (Mooi et al. 1994) and Universal Element Homology (UEH) (Sumrall 2010). The EAT model uses embryological and ontogenetic criteria and designates different kinds of skeletal regions in the echinoderm body as homologous based on developmental and growth patterns; whereas the UEH model attempts to identify individual skeletal plates across clades without reference to regional skeletal patterns. Interestingly, EAT and UEH make different predictions regarding the branching order of major clades in echinoderm phylogeny (cf. David et al. 2000; Kammer et al. 2014) and are sometimes contrasted as alternatives in the literature (Zamora and Rahman 2014). Under the umbrella of Phylogenetic Paleo-ontogeny, these two competing approaches to echinoderm homology become unified. Data supporting EAT and UEH are not mutually exclusive and likely reflect phylogenetic information nested within different hierarchical levels of body plan organization. Paleo-ontogenetic hypotheses for both skeletal regions and individual elemental homologies can be combined into a set of primary homology statements and tested against one another in a future phylogenetic analysis of fossil and living Echinodermata using all available evidence: embryology, ontogeny, genes, and morphology.
I do not propose that combining paleo-ontogenetic character analysis with phylogenetic systematics leads to a more “objective” framework for discovering homology. All propositions of primary homology are necessarily subjective. Indeed, there is no such thing as an assumption free phylogenetic analysis. In science, theories explaining the natural world arise from hypotheses that have survived repeated subjection to a battery of rigorous testing and empirical corroboration. Should we not subject our a priori assumptions behind such “testing” to even greater scrutiny? Phylogenetic empiricism is the basis of evolutionary inference in systematic biology (Wiley and Lieberman 2011). Phylogenetic information is necessarily obscured when a theoretical concept (such as homology) is empirically approximated (phylogenetic analysis), yet how else should science proceed towards asymptotically ascertaining “truth” if not by successive approximation? A research program in Phylogenetic Paleo-ontogeny may help pave the way towards such a future.
References


Figure 2.1 Summary of previously proposed phylogenetic relationships of pancladid crinoids. A, Phylogeny and classification from the *Treatise of Invertebrate Paleontology* based on Moore and Teichert (1978) and Moore et al. (1978). B, A revised phylogeny and classification based on Simms and Sevastopulo (1993), Ausich (1998). C, Phylogenetic relationships according to Webster and Jell (1999).
Fig. 2.1
Figure 2.2 Generalized morphology of cladid crinoids. A, Reconstruction of the Silurian crinoid *Dictenocrinus decadactylus* depicting the morphologic features described in the text. Note that a modern reconstruction would place the crown in a down-current position with the arms in an outstretched position to form a rheophilic filtration fan (modified from Bather 1900, fig. 3). B, Plate diagram of *Dendrocrinus longidactylus* showing the orientation rays and interrays in pan-cladid crinoids. The crinoidal plane of symmetry is interrupted in the posterior region by the addition of plates in the CD interray (modified from Moore et al. 1978, fig. 395). C, The CD interray of three genera depicting common positions and arrangements of posterior plates (modified from Moore et al. 1978, fig. 394). (A-E ray designations in Carpenter’s [1884] system, radials black, radianal cross ruled, anal X and right tube plate [rt] stippled.)
Fig. 2.2
Figure 2.3. An antinomy of alternative primary homology schemes for a single posterior plate in the Mississippian genus *Phanocrinus*. A, Possible homology scheme depicting an evolutionary trend in posterior plate reduction leaving the anal X in the cup. B, An alternative homology scheme depicting the radianal as the single posterior plate. (Redrawn from Strimple [1948]. Radials black, radianal cross ruled, anal X and right tube plate [rt] stippled.)
Fig. 2.3
Figure 2.4 Pentacrinoid stage development and morphogenesis of the extant comatulid crinoid Comactinia meridionalis. A, Early pentacrinoid stage showing the radianal in the C ray with close affinities to the gut tract. B, The radianal is larger than the newly formed C radial and lying obliquely below it. C, Radial plates have increased in size. The radianal has migrated toward the middle of the underlying CD basal while still occupying the inner margin of the C radial plate. D, Radial plates are in lateral contact except in the CD interray, where the radianal occupies a medial position. E, Radial plates are now in complete lateral contact. The radianal has been lifted up within the cup with the growth of the anal tube. F, The radianal rests on the shoulders of the C and D radial plates and continues its upward migration with the anal tube. The radianal is resorbed shortly after this stage. (Stages redrawn from Springer [1920: plate B]. Radials black, radianal cross ruled, AN—anus, B—basal plate, PPCP—primary peristomial cover plate, RA—radianal plate).
Fig. 2.4
Chapter 3: Bayesian estimation of fossil phylogenies and the evolution of early to middle Paleozoic crinoids (Echinodermata)

Abstract.—Knowledge of phylogenetic relationships among species is fundamental to understanding basic patterns in evolution and underpins nearly all research programs in biology and paleontology. However, most methods of phylogenetic inference typically used by paleontologists do not accommodate the idiosyncrasies of fossil data and therefore do not take full advantage of the information provided by the fossil record. The advent of Bayesian “tip-dating” approaches to phylogeny estimation is especially promising for paleo-systematists because time-stamped comparative data can be combined with probabilistic models tailored to accommodate the study of fossil taxa. Under a Bayesian framework, the recently developed fossilized birth–death process (FBD) provides a more realistic tree prior model for paleontological data that accounts for macroevolutionary dynamics, preservation, and sampling when inferring phylogenetic trees containing fossils. In addition, FBD tree prior also allows for the possibility of sampling ancestral morphotaxa. Although paleontologists are increasingly embracing probabilistic phylogenetic methods, these recent developments have not previously been applied to the deep-time invertebrate fossil record. Here, I examine phylogenetic relationships among Ordovician through Devonian crinoids using a
Bayesian tip-dating approach. Results support several clades recognized in previous analyses sampling only Ordovician taxa, but also reveal instances where phylogenetic affinities are more complex and extensive revisions are necessary, particularly among the Cladida. The name Porocrinoidea is proposed for a well-supported clade of Ordovician ‘cyathocrine’ cladids and hybocrinids. The Eucladida is proposed as a clade name for the sister group of the Flexibilia herein comprised of cladids variously considered ‘cyathocrines’, ‘dendrocrines’, and/or ‘poteriocrines’ by other authors.

**Introduction**

Modern macroevolutionary research resides at the nexus of paleontology and phylogenetic comparative biology. The fossil record provides a spectacular temporal window into the vicissitudes of life’s history and paleontologists have long used its patterns to investigate large-scale trends in diversification dynamics and morphologic evolution over timescales inaccessible to experimental manipulation or field-based investigation (Simpson, 1944; Sepkoski, 1981; Hunt et al., 2008; Alroy, 2010). Similarly, biologists armed with molecular phylogenies of extant species and tree-based statistical techniques have increasingly become interested in addressing macroevolutionary questions traditionally studied by paleontologists (e.g., O’Meara et al., 2006; Bokma, 2008; Rabosky, 2009; Rabosky and McCune, 2009; Harmon et al., 2010; Pennell et al., 2014). Although differences between paleontologic and biologic perspectives remain,
attempts to bridge disciplinary gaps between fields have wide-reaching implications for assembling a more synthetic macroevolutionary theory (Jablonski, 2008; Slater and Harmon, 2013; Hunt and Slater, 2016).

Instances of integration between fields, such as paleontology and molecular phylogenetics, often provide opportunities for reciprocal illumination. For example, fossils play a major role in dating divergences among extant species. Without external information to constrain absolute ages, branch length estimation is confounded by the fact that both rates of molecular sequence evolution and elapsed time contribute to observed distances among species. Thus, the construction of a time-calibrated molecular phylogeny requires information on fossil morphologies and their temporal distributions to provide a numerical timescale for testing alternative models of macroevolutionary dynamics (Donoghue and Benton, 2007; Ksepka et al., 2015; dos Reis et al., 2015). Equally illuminating for paleontologists, many probabilistic methods originally developed by molecular phylogeneticists can be modified and applied to paleontologic data (Wagner, 2000a; Wagner and Marcot, 2010; Lee and Palci, 2015; but see Spencer and Wilberg, 2013). For example, Lewis (2001) developed a $k$-state Markov model for calculating likelihoods of discrete, morphologic characters based on a generalization of the Jukes-Cantor model of molecular sequence evolution. Although simplistic, Lewis’ (2001) “Mk” model has recently been demonstrated in a Bayesian context to outperform other phylogenetic methods under a range of conditions present in real datasets, including missing character data, high rates of character evolution (and therefore homoplasy), and rate heterogeneity among characters (Wright and Hillis, 2014; O’Reilly et al., 2016).
recent resurgence of “total-evidence” (Pyron, 2011; Ronquist et al., 2012) approaches in phylogenetics coincides with a renewed interest among biologists in phenotypic evolution and the utility of morphologic phylogenetics in an age of “post-molecular systematics” (Lee and Palci, 2015; Pyron, 2015). This revival of interest in morphologic phylogenetics is good news for paleontologists because nearly all phylogenies of fossil species are inferred using only morphologic character data. Indeed, there has been an increasing number of studies employing probabilistic approaches to estimate phylogenies with morphologic data, especially in paleontology (e.g., Wagner, 1998, 1999; Snively et al., 2004; Pollitt et al., 2005; Clarke and Middleton, 2008; Pyron, 2011; Ronquist et al., 2012; Wright and Stigall, 2013; Lee et al., 2014; Slater, 2013, 2015; Close et al., 2015; Gorscak and O’Connor, 2016; Bapst et al., 2016).

Particularly promising for systematic paleontology is the advent of tip-dating approaches for inferring phylogenies containing non-contemporaneous taxa (Pyron, 2011; Ronquist et al., 2012; Gavryushkina et al., 2014). Bayesian “total-evidence” tip-dating combines molecular sequences, morphologic character data, and temporal information on fossil distributions to simultaneously estimate the best tree topologies, branch lengths, and divergence times among extinct and extant lineages (Ronquist et al., 2012; Lee and Palci, 2015). Tip-dating approaches operate on the simple assumption that evolution can be modeled as a function of time, with either a strict or relaxed clock-like model of character change. Although most tip-dating studies combine fossil and living species (e.g., Pyron, 2011; Ronquist et al., 2012; Slater, 2013), tip-dating approaches equally apply to character matrices containing only morphologic data (Slater, 2015).
and/or with only fossil taxa (Lee et al., 2014; Gorscak and O’Connor, 2016; Bapst et al., 2016). Moreover, mathematical models originally developed for studying the spread of viruses in epidemiology have found applications in fossil tip-dating (Stadler et al., 2012; Stadler and Yang, 2013; Gavryushkina et al., 2014). The “fossilized birth–death” process (Stadler, 2010; Heath et al., 2014) has recently been applied within a Bayesian context as a more realistic tree prior distribution that accounts for macroevolutionary and sampling processes (Gavryushkina et al., 2014).

This paper presents the first application of Bayesian tip-dating methods to a fossil-only dataset of invertebrate animals. Here, I examine phylogenetic relationships among early to middle Paleozoic crinoids (Echinodermata). Crinoids are particularly amenable for the purposes herein because (1) they have a well-sampled fossil record (Foote and Raup, 1996), (2) their skeletal morphology is highly complex and character-rich (Ubaghs, 1978; Foote, 1994; Ausich et al., 2015), and (3) testing phylogenetic hypotheses among crinoid higher taxa requires sampling non-contemporaneous taxa over long timescales (> $10^7$ years), making them an ideal system for implementing a tip-dating approach (Ronquist et al., 2012). Because the approach taken herein is novel to the invertebrate fossil record, I provide a brief discussion on Bayesian tip-dating and the fossilized birth–death process tree prior to familiarize the reader with these emerging methods. Although this makes the paper necessarily technical in places, it is hoped those sections will provide a useful resource for other systematic paleontologists interested in probabilistic approaches to fossil phylogenetics.
Previous work on crinoid phylogeny

The Crinoidea form the sister group to all other extant echinoderm classes (Asteroidea, Echinoidea, Holothuroidea, and Ophiuroidea) and have an extensive geologic history spanning the Lower Ordovician (~480 Ma) to the present day. Ever since Bather (1899) published his seminal work *A Phylogenetic Classification of the Pelmatozoa*, crinoid systematists have sought a robust evolutionary template for understanding the phylogenetic distribution of fossil and living species (Ausich and Kammer, 2001). Other than a few isolated studies conducted at low taxonomic levels (e.g., Kammer, 2001; Gahn and Kammer, 2002), most phylogenetic research using computational methods have focused on inferring relationships within two key time intervals: the Ordovician and the Recent (Ausich, 1998; Guensburg, 2012; Hemery et al., 2013; Rouse et al., 2013; Ausich et al., 2015; Summers et al., 2014; Cole, in press). These intervals are significant because they bookend the evolutionary history of crinoids into their early diversification during the Ordovician Period and their present day diversity in marine ecosystems. However, these intervals are separated by ~480 million years and phylogenetic research linking post-Ordovician stem taxa with the crown Crinoidea remains a largely unexplored area of research (Simms, 1988; Simms and Sevastopulo, 1993; Webster and Jell, 1999).

Crinoids are traditionally divided into several higher taxa, including the Camerata, Disparida, Hybocrinida, Cladida, Flexibilia, and the Articulata (Moore and Teichert, 1978). Except for articulate crinoids, these groups first appear in Ordovician rocks. Despite more than a century of controversy, phylogenetic relationships among
Ordovician taxa are reaching a consensus. For example, all recent analyses of Ordovician crinoids strongly support an early divergence between camerate and non-camerate crinoids (Guensburg, 2012; Ausich et al., 2015; Cole, in press). Thus, the Camerata is the sister clade to all non-camerate crinoids. Similarly, both Guensburg (2012) and Ausich et al. (2015) recovered a monophyletic Hybocrinida as the sister clade to a subset of cladid taxa. Ordovician analyses also recover a monophyletic Disparida as sister to the clade of cyathocrine cladids and hybocrinids (Guensburg, 2012; Ausich et al., 2015). However, relationships among taxa placed currently within the Cladida, and their relationships to other higher taxa, have been a long-standing problem in crinoid systematics (McIntosh, 1986, 2001; Sevastopulo and Lane, 1988; Simms and Sevastopulo, 1993; Kammer and Ausich, 1992, 1996).

In his review of echinoderm phylogeny and classification, Smith (1984) lamented the cladid portion of the crinoid tree was one of the “outstanding areas of ignorance in echinoderm phylogeny” (Smith, 1984, p. 456). Indeed, the Cladida (sensu Moore and Laudon, 1943) have long been considered a paraphyletic group because some nominal cladids are hypothesized to be more closely related to flexible and/or articulate crinoids than other cladids (Springer, 1920; Simms and Sevastopulo, 1993; Brower, 1995; Ausich, 1998; Wright, 2015). Unfortunately, recent phylogenetic analyses not only confirm that Ordovician cladids are a paraphyletic assemblage (Guensburg, 2012; Ausich et al., 2015), but also that the validity of the Cladida and their constituent higher taxa (i.e., Dendrocrinida and Cyathocrinida) cannot be fully remedied by simply adopting Simms and Sevastopulo’s (1993) recommendation to place the Flexibilia and Articulata within
the Cladida. In addition, because the monophyletic status of a taxon requires a temporal reference frame (conventionally taken as the present day), it is unknown whether some recovered “clades” in Ordovician analyses retain their monophyletic status when younger taxa are considered. For example, Ordovician cyathocrine cladids are typically recovered as a clade (Ausich, 1998; Ausich et al., 2015), but are sometimes nested within a more inclusive clade of cyathocrines and hybocrinids when hybocrinids are sampled in the same analysis. Testing whether or not the other cyathocrine cladids belong to this clade remains an open question and requires sampling younger species. Similarly, Ordovician cladids placed within the Dendrocrinida (sensu Moore and Laudon, 1943) are paraphyletic, but there may nevertheless be latent phylogenetic structure present among subsets of post-Ordovician dendrocrines that could inform taxonomic revisions.

The analyses conducted herein build on and further test recently proposed phylogenetic hypotheses that sample only Ordovician crinoids (Guensburg, 2012; Ausich et al., 2015). Thus, this analysis includes a broad sample of early to middle Paleozoic (Ordovician–Devonian) non-camerate crinoids and primarily focuses on resolving relationships among the problematic Cladida.

**Bayesian phylogenetics and the fossilized birth-death process**

Bayesian phylogenetic methods combine a likelihood model of evolution with a set of prior probabilities to generate a posterior probability distribution of phylogenetic trees.
and their associated parameters. The Bayesian framework used herein is adapted from Gavryushkina et al. (2015). This model uses time-stamped morphologic character data to simultaneously estimate a posterior distribution of phylogenetic trees, divergences times, and other macroevolutionary and sampling parameters.

Let $\Psi$ be a phylogeny (i.e., tree topology with branch lengths in units of time), $\delta$ be a vector of parameters describing morphologic evolution, and $\pi$ be the tree prior (and its associated hyper parameters). Using Bayes theorem, the posterior probability distribution is,

$$f[\Psi, \pi, \delta|X, d] = \frac{f[X|\Psi, \delta]f[d|\Psi]f[\Psi|\pi]f[\pi]f[\delta]}{f[X, d]},$$

where $X$ is a character by taxon matrix of morphologic character data and $d$ is a vector of age ranges for each fossil taxon. The numerator on the right hand side of the equation can be separated into the tree likelihood function, $f[X|\Psi, \delta]$, and the remaining terms, which comprises the prior. Equations for calculating $f[X|\Psi, \delta]$ are well described in literature and therefore a disquisition on tree likelihoods is not presented here. Interested readers are advised to see summaries in Swofford et al. (1996), Lewis (2001), Felsenstein (2004), and Yang (2014). The density $f[\Psi|\pi]$ describes the tree prior (see below) and $f[d|\Psi]$ is the density of obtaining fossil occurrence ranges given $\Psi$ (this term is treated herein as a constant, see Gavryushkina et al., 2015). The denominator $f[X, d]$ is a
normalizing constant and is equal to the marginal probability of the data. Given the necessary inputs, the posterior distribution of trees is estimated using a numerical technique called Markov chain Monte Carlo (MCMC) that eliminates the need to calculate $f[X, d]$ when estimating the posterior distribution of trees.

A great strength of the Bayesian paradigm is that sources of uncertainty can be explicitly incorporated into the evolutionary model via the use of prior distributions on pertinent parameters (Heath and Moore, 2014). For example, numerous factors can influence and potentially distort the accuracy of reconstructed evolutionary trees—arguably the most important parameter in phylogenetic inference. Even in cases where these other factors are not of primary interest, acknowledging and estimating “nuisance parameters” is nevertheless important because it reduces the chance that any particular incorrect assumption will lead to the recovery of specious tree topologies (Huelsenbeck et al., 2002; Wagner and Marcot, 2010; Gavryushkina et al., 2014). Potential biasing factors may include variation in rates of morphologic evolution, taxonomic diversification rates, ancestor-descendant relationships, and (incompletely) sampling taxa over time rather than from a single time slice (Smith, 1994; Wagner, 2000b, 2000c; Wagner and Marcot, 2010; Bapst, 2012). Variability in evolutionary rates can be modeled with prior distributions to describe rate variation among characters. Similarly, rate variation among lineages can be modeled using uncorrelated ‘relaxed clock’ models where branch-specific rates are independently drawn from the same underlying parametric distribution (Lepage et al., 2007; Heath and Moore, 2014).
Bayesian inference weights the likelihood of a tree by its prior probability. The fossilized birth-death (FBD) process (Stadler, 2010; Didier et al., 2012; Heath et al., 2014) is an extension of the constant rate birth-death models commonly used in paleontology (e.g., Raup et al., 1973; Raup, 1985) and considers fossil preservation in addition to diversification dynamics. Below, I briefly describe the FBD process as a tree prior and argue it is well-suited to accommodate these additional sources of concern.

Tree prior.—The fossilized birth–death (FBD) process is a stochastic branching model for describing macroevolutionary dynamics, fossil preservation, and sampling (Stadler, 2010; Heath et al., 2014). The FBD processes begins at some time $t_0 > 0$ in the past and ends when $t = 0$. As time moves forward (i.e., decreasing toward the “present”), each lineage may probabilistically undergo one of three process-based events, each according to a distinct constant rate Poisson process: branching (i.e., lineage splitting via speciation) with rate $p$, extinction with rate $q$, or fossil preservation and sampling with rate $r$ (Stadler, 2010; Heath et al., 2014). Lineages alive at the end of the process are sampled with probability $\varepsilon$ corresponding to the sampling fraction of “extant” taxa. Importantly, the start and end times for the FBD process are arbitrary and time can therefore be shifted to accommodate temporal frameworks more commonly used in paleontology. For example, paleontological systematists working on entirely extinct groups (e.g., trilobites) or sampling taxa from a restricted temporal interval (e.g., Paleozoic crinoids) can shift time such that $t = 0$ corresponds to the age of the youngest species sampled. The FBD process represents a major advance over other birth-death models in paleontology (e.g., Raup,
1985) because fossil preservation and sampling issues are modeled in addition to clade diversification. In Gavryushkina et al.’s (2014) implementation, a lineage may be sampled more than once, thereby producing an internal node connected to only two (rather than three) branches. A two-degree internal node in a phylogenetic tree implies a hypothesized ancestor-descendant relationship, via direct or indirect ancestry (Fig. 3.1) (Foote, 1996; Gavryushkina et al., 2014, 2015).

The set of stochastic branching, extinction, and sampling events for a single FBD process gives rise to a “complete” phylogeny with generating parameters \( \pi = (p, q, r, \varepsilon, t_o) \). The “sampled” FBD phylogeny is obtained when all lineages with unsampled descendants produced by the process are pruned from the tree and therefore represents the reconstructed tree topology and divergence times implied by the sampled taxa (Fig. 3.1). Trees sampled from the FBD process are called sampled ancestor phylogenetic trees (even if no ancestors were sampled) and their nodes can be labeled to summarize their unique history of macroevolutionary and sampling events (Gavryushkina et al., 2014).

Equations for calculating the probability density of \( f(\Psi|\pi) \) given the FBD parameters \( p, q, r, \) and \( \varepsilon \) can be derived by modifying birth-death sampling models used to study virus transmissions in epidemiology (Stadler, 2010; Stadler et al., 2012; Gavryushkina et al., 2014; Zhang et al., 2016) and their details are discussed in supplemental information at the end of this chapter.
Taxon sampling, characters analyzed, and specimens examined

The character matrix analyzed herein was constructed as part of a larger project resolving phylogenetic relationships among Paleozoic crinoids. I updated, modified, and expanded the character list of Ausich et al. (2015) to include an ensemble of new characters to better capture variation among post-Ordovician taxa, particularly among ‘cladids’ (Ausich et al., 2015; Wright and Ausich, 2015). Because the taxonomic diversity of fossil crinoids is formidable high for comprehensive analysis, taxon sampling was restricted to Ordovician through Devonian species and multiple exemplars were sampled at pertinent taxonomic scales appropriate to the present analysis (Brusatte, 2010). The matrix was constructed in an attempt to maximize sampling across the broad spectrum of taxonomic, morphologic, and preservation gradients while keeping rigorous analysis tractable (Wagner, 2000b; Carlson and Fitzgerald, 2007; Heath et al., 2008).

The dataset contains representative species from Ordovician, Silurian, and Devonian families of nominal ‘cladids’ (including cyathocrines and dendrocrines), disparids, hybocrinids, and flexibles (all taxa sensu Moore and Laudon, 1943). Species chosen as exemplars were typically the type species of a type genus that well-characterize the distribution of morphologic traits for each higher taxon, but sometimes geologically older species and/or more complete specimens were sampled instead (Table 1). Characters, plate homologies, and terminology are after Ubaghs (1978) and Ausich et al. (2015), with updates from Webster and Maples (2006) and Wright (2015). All but four traits were treated as unordered binary or multistate characters (Supplemental Data 1).
These four characters were ordered based on known patterns of crinoid development and arguments for ordering these traits are discussed in Wright (2015) and Webster and Maples (2006, 2008). Unknown and inapplicable character states were coded as missing. This new compilation of more than 3,000 specimen-based observations is the largest and most comprehensive morphologic data matrix ever constructed sampling Ordovician and post-Ordovician fossil crinoids (Supplemental Data 2).

In the final matrix, a total of 87 discrete morphologic characters comprising more than 300 character states were sampled across 42 species of non-camerate crinoids (Supplemental Data 2). Camerates were not included in the analysis because they diverged from non-camerate crinoids by at least the earliest Ordovician (Guensburg and Sprinkle, 2003; Guensburg, 2012; Ausich et al., 2015; Cole, in press). Although tip-dating analyses do not per se require use of an outgroup (Ronquist et al., 2012), there are several reasons I used the Tremodocian species Apektocrinus ubaghsi Guensburg and Sprinkle, 2009 to assist rooting the tree. Apektocrinus was originally described as a tentative cladid that featured traits intermediate between protocrinoids and nominal cladids (Guensburg and Sprinkle, 2009). Protocrinoids were originally considered basal crinoids stemward of the divergence between camerates and non-camerates (Guensburg and Sprinkle, 2003). However, Guensburg (2012) subsequently placed protocrinoids within the Camerata and later analyses by Ausich et al. (2015) recovered protocrinoids to be closer to non-camerates than camerates. Regardless of the labile phylogenetic position of protocrinids, both Guensburg (2012) and Ausich et al. (2015) recovered tree topologies with Apektocrinus as the sister taxon to the clade comprised of non-camerate crinoids.
Thus, the early stratigraphic position, mosaic distribution of plesiomorphic and apomorphic traits, and strong support from previous phylogenetic analyses all indicate Apektocrinus occupies a position near the base of the non-camerate tree (Guensburg and Sprinkle, 2009; Guensburg, 2012; Ausich et al., 2015).

Matrix construction required extensive first-hand examination of well-preserved specimens housed in museum collections and the published taxonomic literature. When possible, I coded characters from direct observations of type-series specimens for each species. Although emphasis was placed on observing characters from type specimens, non-type specimens were also examined to ensure the character distributions for each species were coded as completely as possible. Specimens were examined from collections within the United States National Museum of Natural History; the Field Museum of Natural History, the Lapworth Museum of Geology, and the Natural History Museum (London).

**Phylogenetic analyses**

Bayesian phylogenetic analyses were conducted using Markov chain Monte Carlo (MCMC) sampling in the MPI-version of MrBayes 3.2.5 (Ronquist et al., 2012), which implements MCMC proposals for FBD trees (Zhang et al., 2016). To account for differences among alternative model configurations, multiple phylogenetic analyses were conducted and Bayes Factors (BF) were calculated to statistically compare models.
Bayes Factors are used in Bayesian model selection to determine which parameter configurations provide the best fit to the data and are equal to twice the difference in marginal log-likelihoods between models (Kass and Raftery, 1995). Following phylogenetic analyses, I then estimated the marginal log-likelihood of each model using the stepping-stone sampling method (Xie et al., 2010) with 50 steps and powers of $\beta$ corresponding to quantiles of a Beta(0.5, 1.0) distribution. Parsimony-based calculations were performed using PAUP* 4.0a147 (Swofford, 2002). All additional analyses were conducted using custom scripts written in the R statistical computing environment making use of functions from the packages ape (Paradis et al., 2004), and strap (Bell and Lloyd, 2015). Details regarding choices of prior distributions, constraints, and MCMC convergence are discussed below.

Morphologic character evolution was modeled using the Mk model with equal transition frequencies among character states and a correction for ascertainment bias in character acquisition (Lewis, 2001). The distribution of rates among characters can assume either a uniform “equal rates” model or explicitly account for rate heterogeneity using a skewed parametric distribution. A preliminary parsimony-based estimation of rate variation in the crinoid character matrix depicts a highly skewed distribution (Fig. 3.2); strongly suggesting it is unwise to assume a model of equal rates of change among characters. This is particularly striking given that parsimony-based rate distributions tend to underestimate morphologic changes and are therefore slightly biased toward equal rates (Harrison and Larsson, 2015). To further test this hypothesis, I conducted separate analyses assuming equal, lognormal, and gamma distributed rates of character change.
Following Harrison and Larsson’s (2015) recommendation, analyses with gamma or lognormal variation used eight instead of four discrete rate categories (commonly applied to molecular data).

Fossil tip-dating requires a model characterizing the distribution of evolutionary rates throughout the tree. The case of a strict-morphologic clock assumes rates are constant among lineages. However, the assumption of the strict-clock can be “relaxed” by allowing rates to vary among branches throughout the tree (Lepage et al., 2007; Heath and Moore, 2014). To test whether evolutionary rates vary among lineages, analyses using strict and relaxed-clock analyses were conducted. The independent gamma rates (IGR) relaxed-clock model was applied to account for variation in rates among branches. The IGR model facilitates episodic “white noise” variation in rates across the tree and is appropriate because large-scale morphologic evolution is a function of both waiting times and stochastic selective forces (Wagner, 2012; Heath and Moore, 2014). A lognormal distribution was placed on the base-rate of the clock using methods outlined in Ronquist et al. (2012).

A key assumption of tip-dating is that evolutionary change is a function of time. In other words, geologically younger species are expected to have undergone a greater amount of within-lineage evolution (i.e., anagenesis) than older species because more time has elapsed for changes to occur (Smith et al., 1992; Wagner, 2000a). To test whether this assumption holds (and therefore whether or not the tip-dating method is valid for these data), the parsimony-based root-to-tip pathlength of each species from a
non-clock analysis was regressed against median age dates from the IGR analysis using both phylogenetically corrected and uncorrected methods (Lee et al., 2014).

The FBD process was used as a tree prior (i.e., “samplestrat = random” in MrBayes 3.2.5). The implementation of the FBD in MrBayes reparameterizes the FBD process in terms of net diversification \( (= p - q) \), turnover \( (= q / p) \), and sampling probability \( (= r / (q + r)) \). I placed an Exp(1) prior on net diversification, a Beta(1,1) uniform prior on turnover, and a Beta(2,2) prior on the sampling probability. To account for uncertainty in divergence time estimation, age ranges for fossil species were given broad uniform distributions typically corresponding to the stratigraphic range of their higher taxon and were taken from an updated version of Webster’s (2003) index of Paleozoic crinoids (Supplemental Data 2). Because the age of the most recent common ancestor of all species in the analysis is well-constrained by fossil evidence to be near the base of the Ordovician, the tree age prior was fixed to correspond to the earliest Tremadocian.

Tip-dating is a computationally demanding phylogenetic method that requires a time-consuming exploration of parameter space. To assist the analysis, several topological constraints were applied to reduce MCMC exploration of very unlikely trees and to test more specific phylogenetic hypotheses (see Guillerme and Cooper, 2016). For example, the monophyly of disparids and flexibles are well-supported by other studies (Brower, 1995; Ausich, 1998; Guensburg, 2012; Ausich et al., 2015) and preliminary analyses. Thus, their status as clades is not in question. However, the branching positions of these clades within the larger crinoid tree remain an open question and their phylogenetic
placement is evaluated herein. A partial constraint was placed on *Eustenocrinus, Iocrinus, Ibexocrinus, and Heviacrinus* that allowed for either *Merocrinus* and/or *Alphacrinus* to be included within the disparid clade if the data support that hypothesis. This was done because whether *Merocrinus* is closer to cladids or disparids requires additional testing (cf. Ausich, 1998; Guensburg, 2012). *Alphacrinus* is a stratigraphically old taxon with a combination of unique and disparid-like traits that may or may not be stemward to ingroup Disparida (Guensburg, 2010). A hard constraint was placed on a flexible clade comprised of *Homalocrinus, Icthyocrinus, Lecanocrinus, Protaxocrinus, and Sagenocrinites*.

Markov chain Monte Carlo analyses consisted of two independent runs of four chains sampling every 4000 generations for 40 million generations per run with a burn-in percentage of 35%. Convergence was assessed using multiple criteria: average standard deviation of split frequencies among chains were below 0.01 (< 0.05 for some IGR analyses) (Gelman and Rubin, 1992), potential scale reduction factors of ~1.0 (Lakner et al., 2008), effective sample sizes greater than 300 (with many > 1000), and visual inspection of log-likelihoods plots among runs using Tracer v.1.6 (Drummond and Rambaut, 2007). Finally, the analysis with the best fit parameter settings was repeated three times to ensure estimates of optimal tree topologies were robust across runs. Together, these diagnostics indicate convergence among tree topologies and parameter estimates.

To summarize the posterior distribution of tree topologies, I generated a maximum clade credibility tree (MCC) using TreeAnnotator (Rambaut and Drummond,
Although there is no single agreed upon method for summarizing Bayesian posterior distributions of phylogenetic trees (Heled and Bouckaert, 2013), posterior probability can be viewed as an optimality criterion in phylogenetic inference (Rannala and Yang, 1996; Huelsenbeck et al., 2002; Wheeler and Pickett, 2007; Wheeler, 2012; Rambaut, 2014). The MCC tree is the tree in the posterior distribution with the maximum product of clade posterior probabilities and represents a Bayesian point estimate of phylogeny (Rambaut, 2014).

I also ran a series of sensitivity analyses \((n > 5)\) to explore the effects of choosing different priors, including the prior placed (1) on the variance of the gamma distribution in the IGR model, and (2) on the FBD turnover \((= q / p)\) parameter. In all cases, statistically indistinguishable median estimates were obtained for node ages, branch lengths, and FDB parameters. In addition, I calculated the pairwise Robinson-Foulds (RF) distance (Robinson and Foulds, 1981) within and among tree distributions from separate analyses and ordinated the resulting RF matrix using principal coordinate analysis. A visual inspection of RF distances in principal coordinate space reveals substantial overlap between distributions, with no obvious gradient or isolated “islands” (analogous to Maddison, 1991) of trees. Thus, the analysis presented herein is considered robust across a range of possible prior configurations.
Results

The relationship between within-lineage morphologic evolution and IGR age estimates indicate early to middle Paleozoic crinoids conform well to the assumptions of tip-dating. Parsimony-based branch lengths from a non-clock analysis reveals geologically younger taxa have higher amounts of anagenesis compared to older taxa ($p = 0.017$) (Fig. 3.3). This relationship holds even when accounting for phylogenetic non-independence among comparisons, as phylogenetic independent contrasts (Felsenstein, 1985) also reveal a strong statistical association between branch durations (in the best-fit IGR analysis) and morphologic divergence (measured in parsimony steps from an undated analysis) ($p = 0.005$) (see Lee et al., 2014).

Bayes Factors provide evidence for heterotachy in crinoid evolution throughout this interval (Supplemental Data 3). The equal rates model of character evolution was strongly rejected in favor of models incorporating rate variation (BF = 166.42 for lognormal, BF = 162.04 for gamma), with the lognormal slightly outperforming a gamma distribution (BF = 4.38). Similarly, the strict-morphologic clock was strongly rejected in favor of the IGR relaxed-clock model accounting rate variation among lineages (BF = 54.56).

The MCC tree from the best fit model is presented in Figure 3.4. Although posterior probabilities for some clades are low, they are comparable to other tip-dating studies using morphologic characters (Lee et al., 2014; Gavryushkina et al., 2015; Gorscak and O’Connor, 2016). Because Bayesian analyses account for uncertainty in the
phylogenetic placement of taxa, it is important to stress that relationships depicted in Figure 3.4 are not the only ones supported in the posterior distribution. However, MCC tree topologies were broadly consistent across all analyses, indicating topological results are robust across different model configurations. Keeping uncertainty in mind, there are many salient features of the MCC tree that support previous phylogenetic hypotheses and throw light on several taxonomic questions.

The base of the MCC tree is characterized by a basal divergence between disparids (and disparid-like taxa) and all other non-camerate crinoids. Neither *Merocrinus* nor *Alphacrinus* were placed within the clade comprised of *Iocrinus*, *Ibexocrinus*, *Eustenocrinus*, and *Heviacrinus*. However, *Merocrinus* is placed as the sister taxon to *Metabolocrinus*, which together form a sister to the above mentioned disparid clade. Interestingly, *Alphacrinus* is placed as the sister taxon to the clade comprised of *Merocrinus*, *Metabolocrinus*, and disparids, which supports Guensburg’s (2010) original hypothesis of *Alphacrinus* being a basal disparid-like taxon and contrasts with Guensburg’s (2012) subsequent analysis recovering *Alphacrinus* as nested within the disparid clade.

Similar to other studies (Ausich, 1998; Guensburg, 2012; Ausich et al., 2015), a clade comprised of cladids and hybocrinids was recovered. This clade is strongly supported with posterior probability 0.96. The hybocrinids *Hybocrinus* and *Hybocystites* are sister taxa and occupy a nested position within a clade of dicyclic ‘cyathocrine’ cladids (i.e., *Carabocrinus* and *Porocrinus*), suggesting these taxa are pseudomonocyclic (Sprinkle, 1982; Guensubrg, 2012; Ausich et al., 2015).
A clade comprised of *Cupulocrinus* and flexible crinoids was recovered as sister to a clade comprised of only cladids, with the inclusive clade supported with posterior probability 0.65. Although *Cupulocrinus* is a nominal cladid (sensu Moore and Laudon, 1943), it is placed closer to flexibles than other cladids in 96% of trees in the posterior distribution.

The large clade comprising the most recent common ancestor of *Plicodendrocrinus* and *Corematocrinus* and its descendants contains a scattering of taxa traditionally placed within the cladid orders Cyathocrinida and Dendrocrinida (sensu Moore and Laudon, 1943). Thus, the traditionally recognized ‘cyathocrine’ and ‘dendrocrine’ cladids represent evolutionary grades of body plan organization rather than clades. For example a clade of cyathocrine-grade crinoids containing the most recent common of *Thalamocrinus* and *Gasterocoma* is supported with posterior probability 0.80, with subclades supported by posterior probabilities between 0.53–0.75. Similarly, a different clade containing the most recent common ancestor of *Lecythocrinus* and *Petalocrinus* also features ‘cyathocrine’ morphologies. These results support (perhaps unfortunately) long-held suspicions of taxonomic anarchy among cladids recognized by previous authors (McIntosh, 1986; 2001; Simms and Sevastopulo, 1993; Kammer and Ausich, 1992, 1996; Webster and Maples, 2006).

The clade of dendrocrine-grade crinoids containing the most recent common ancestor of *Thenarocrinus* and *Corematocrinus*, and its constituent subclades, are supported with posterior probabilities between 0.68–0.84. This clade contains a subclade comprised of members of the Rutkowskicrinidae, Glossocrinidae, Corematocrinidae, and
Amabilicrinidae. This clade is supported with posterior probability 0.84 and is equivalent to the Superfamily Glossocrinacea originally recognized by Webster et al. (2003).

Discussion

It is generally appreciated that quantitative phylogenetic methods do not typically take full advantage of the complete spectrum of information supplied by the fossil record (Wagner and Marcot, 2010). However, recently developed probabilistic macroevolutionary models and powerful computational tools have provided major advancements for estimating phylogenies containing fossil taxa and accommodating paleontologic idiosyncrasies, such as sampling taxa (incompletely) over time (Stadler, 2010; Ronquist et al., 2012; Gavryushkina et al., 2014; Lee and Palci, 2015). This paper builds on these advances by implementing a Bayesian framework to estimate time-scaled phylogenetic hypotheses of early to middle Paleozoic fossil crinoids. The resulting phylogeny indicates extensive taxonomic revisions are necessary, especially among the ‘cladid’ crinoids, and points to several areas where further analysis at lower taxonomic levels is needed. In addition to evolutionary implications for crinoids, the results also raise several key issues regarding probabilistic approaches to phylogenetic inference in the fossil record and suggest possible directions for future research.
Implications for crinoid evolution and systematics.—The phylogenetic analysis presented herein offers several insights into early to middle Paleozoic crinoid evolution and provides a basis for requisite taxonomic revisions. Although I provide suggestions for revisions below, attempting to more fully resolve outstanding problems in crinoid systematics and classification is beyond the scope of this paper. Instead, that topic is addressed in a companion paper (see Wright et al., in press).

A basal divergence between disparids and most other non-camerate crinoids has been recovered in a number of recent phylogenetic studies (cf. Guensburg, 2012; Ausich et al., 2015), including the analysis herein. Although several nominal ‘cladids’ are stemward of this split (see Ausich et al., 2015, fig. 5), the overwhelming majority of nominal cladids (sensu Moore and Laudon, 1943) are not. Thus, disparids are nested within a clade comprised of the common ancestor of all nominal ‘cladids’ (sensu Moore and Laudon, 1943) and all of its descendants. Following Simms and Sevastopulo (1993), the Flexibilia and Articulata are placed within the Cladida, but no previous phylogenetic hypothesis has considered the Disparida a subclade within the Cladida. In an effort to retain as much of the original intent and traditional use of taxonomic names as possible, a re-definition of the Cladida is necessary to prevent the Disparida from being considered a subclade of cladids, particularly since the Cladida is already in need of extensive revision for other reasons. A simple solution to remedy the problem could be obtained using phylogeny-based clade definitions that recognize the Disparida and Cladida (sensu Simms and Sevastopulo, 1993) as sister clades. This would require orphaning only a small number of so-called ‘cladids’ (sensu Moore and Laudon, 1943) as stem taxa to the
Disparida + Cladida clade and retain the majority of cladids (sensu Moore and Laudon, 1943) within the more inclusive Cladida (sensu Simms and Sevastopulo, 1993). The Disparida is considered herein to include the most recent common ancestor of *Alphacrinus* and *Eustenocrinus*. Thus, *Merocrinus* and *Metabolocrinus* (typically considered cladids [Ausich, 1998], but see Guensburg, 2012) are tentatively placed within the disparid clade (Fig. 3.4), but further work and character-based analyses are needed to confirm the precise phylogenetic position of these problematic taxa. A more comprehensive discussion with rigorous phylogenetic definitions and a revised classification for cladid and disparid clades is provided in Wright et al. (in press).

Previous analyses of Ordovician taxa have recovered monophyletic groups, such as a clade comprised of cyathocrine cladids and hybocrinids (Guensburg, 2012; Ausich et al., 2015). This offered some hope that potentially the Cyathocrinida might be monophyletic (Ausich, 1998; Guensburg, 2012; Ausich et al., 2015). However, the present analysis rejects the monophyly of the Cyathocrinida because some nominal cyathocrines are more closely related to nominal dendrocrines than to other cyathocrines. If these results are taken seriously, then an extensive revision of higher taxa within the Cladida is needed. To further test this issue, I conducted an additional analysis placing a hard topological constraint on all cyathocrine cladids (see Bergsten et al., 2013). Comparing this analysis to the best fit model described above, Bayes Factors strongly reject a model where cyathocrines are forced to be monophyletic (BF = 9.64). Thus, caution should be exercised when extrapolating results from an analysis considering one timeslice to subsequent time intervals. Nevertheless, there is strong support for a clade of
cyathocrine-grade cladids and hybocrinids (Ausich, 1998; Guensburg, 2012; Ausich et al., 2015). This clade is characterized by a number of morphologic features convergent with blastozoan echinoderms, such as thecal respiratory structures, calyx and/or arm plate reduction, and recumbent ambulacra. Given the strong statistical support and morphologic distinctness of this clade, I propose the name Porocrinoidea to represent this idiosyncratic group of crinoids. The Hybocrinida is considered herein a subclade within the Porocrinoidea (Fig. 3.4).

The position of *Cupulocrinus* at the base of the flexible clade has strong statistical support and corroborates earlier studies linking *Cupulocrinus* with flexible crinoids (Springer, 1911, 1920; Brower, 1995; Ausich, 1998) (Fig. 3.4). For example, Springer (1920) considered *Cupulocrinus* to have traits intermediate between cladids and flexibles and hypothesized a species of *Cupulocrinus* was ancestral to the Flexibilia. Because phylogenetic relationships were estimated using methods that include the possibility of potentially sampling ancestral morphotaxa, Springer’s (1920) hypothesis can be quantitatively addressed. The posterior probability of a taxon being a sampled ancestor can be estimated as the frequency in which it was recovered to have a zero-length branch in the posterior distribution of trees (Matzke, 2015). Examining the posterior distribution of trees from the best-fit model, the probability of *Cupulocrinus humilis* (Billings, 1857) being an ancestral morphotaxon is 0.99. Given that a clade is defined to be an ancestor and all of its descendants, *Cupulocrinus* is removed from the Cladida and placed within the Flexibilia. Additional analyses with more comprehensive sampling of *Cupulocrinus*
and flexible species (including a broader sample of taxon-specific characters) are needed to further test this hypothesis at finer taxonomic scales.

The sister clade to the Flexibilinia contains the majority of all nominal taxa currently placed within the Cladida (sensu Moore and Laudon, 1943). This clade originated prior to the close of the Ordovician and contains most taxa traditionally placed within the orders Dendrocrinida and Cyathocrinida. Notably, all species in this clade share a more recent common ancestor with an extant crinoid than with flexible crinoids (Simms and Sevastopulo, 1993). Thus, I propose the name Eucladida to distinguish this important group of crinoids from their sister clade.

The recovery of the Glossocrinacea as a clade provides quantitative support for evolutionary inferences discussed in Webster et al. (2003). These “transitional dendrocrinids” (McIntosh, 2001) are among the first cladids to evolve pinnules and are traditionally placed within the Order Poteriocrinida. Most crinoid workers since publication of the Treatise of Invertebrate Paleontology (Moore and Teichert, 1978) have hesitated to recognize the Poteriocrinida because they are widely considered to be polyphyletic (Kammer and Ausich, 1992; McIntosh, 2001). Regardless of their status as a clade or a grade, the crinoids considered poteriocrines in the Treatise are the most dominant and ecologically abundant group of crinoids throughout the middle to late Paleozoic (Ausich et al., 1994). Notably, the ancestor of extant articulate crinoids is widely considered to be placed among a paraphyletic group of ‘poteriocrine’ crinoids (Simms and Sevastopulo, 1993; Webster and Jell, 1999; Rouse et al., 2013). The recovery of a clade of poteriocrines herein suggests there may be some phylogenetic structure.
present among Paleozoic poteriorcrine taxa. However, future analyses sampling younger taxa and a broader sample of Treatise (Moore and Teichert, 1978) poteriocrines are needed to test whether this is the case.

_Probabilistic approaches to fossil phylogenies._—Tree-based comparative methods are becoming commonplace in paleontology for testing macroevolutionary patterns and processes within a fully phylogenetic context. To date, most of these studies apply an a posteriori timescaling algorithm to an unscaled cladogram (e.g., Brusatte et al., 2008; Hunt and Carrano, 2010; Lloyd et al., 2012; Hopkins and Smith, 2015). Although useful for removing the zero-length branches that arise from polytomies in cladistic hypotheses, many of these a posteriori timescaling methods are problematic because they make ad-hoc and unrealistic assumptions regarding node ages and/or ancestor-descendant relationships (Bapst and Hopkins, in press). The _cal3_ method developed by Bapst (2013) is a promising a posteriori approach that overcomes many of these problems via a model of branching, extinction, and sampling similar to the FBD process. However, this technique requires a priori estimates of these parameters and can only be applied to unscaled cladograms. The Bayesian tip-dating approach advocated herein simultaneously estimates tree topologies and divergence dates using time-stamped comparative data. Thus, a sample of trees from the posterior distribution of a tip-dated analysis provides a more natural framework for testing macroevolutionary patterns using the fossil record while accounting for uncertainty in tree topology and node ages (Close et al., 2015; Gorscak and O’Connor, 2016).
Evaluating the efficacy of competing phylogenetic methods is a contentious (and sometimes acrimonious) debate, yet inferences using simple probabilistic methods perform well when inferring trees from paleontologic data and can explicitly consider different evolutionary and sampling parameters potentially influencing recovered topologies (Wagner, 1998; Wagner and Marcot, 2010; Wright and Hillis, 2014). Thus, it seems that in the future more phylogenetic analyses will take advantage of fully probabilistic frameworks such as the one presented herein. However, researchers conducting tree-based comparative analyses on older (or otherwise unscaled) cladograms require an a posteriori time-scaling approach, which might take the form of applying FBD-like divergence dating methods to a fixed cladistic topology (Bapst and Hopkins, in press). Regardless of whether Bayesian tip-dating or a model-based a posteriori method like cal3 becomes the dominant approach to timescaling trees in the future, it is apparent that both of these approaches recover more accurate estimates and are strongly recommended over ad-hoc methods when conducting downstream macroevolutionary analyses.

Evolutionary patterns among early to middle Paleozoic crinoids strongly favor models incorporating rate heterogeneity among characters and among lineages. This not only supports previous investigations demonstrating differential disparity patterns among crinoid clades (Foote, 1994; Deline and Ausich, 2011), but may also be a more general feature of morphologic evolution. Probabilistic models of morphologic evolution commonly assume either uniform or gamma distributed rates among characters. Models of rate variation predict some characters evolve at higher rates than others (and therefore
anticipate a degree of homoplasy in the data). Variable rate distributions are potentially more realistic than an equal rates model because morphologic characters commonly experience different selective pressures and/or developmental constraints. Moreover, accounting for rate variation has a practical value because it may help resolve branches at different levels in a phylogenetic tree (Wright and Hillis, 2014).

Until recently, only uniform and gamma distributions were available to model among character rate variation in common software packages for Bayesian inference (Huelsenbeck et al., 2015). However, Wagner (2012) found that fossil datasets commonly favor lognormal rather than gamma distributed rates, particularly for echinoderm and mollusc character matrices. Interestingly, gamma and lognormal rate distributions arise from different underlying processes of character evolution. Gamma rate distributions assume rates are Poisson processes, whereas lognormal rate distributions suggest morphologic evolution results from multiple probabilistic processes and/or hierarchical integration among characters (Wagner, 2012). Thus, the relative fit of the data to these two distributions gives some insight into the dynamics of character change. The analysis herein provides positive evidence supporting lognormal over gamma-distributed rates, but only modestly (BF = 4.38). Although the choice of rate distribution had no obvious effect on recovered topologies herein, other workers should nevertheless test alternative distributions and choose the best fit model for their data (Harrison and Larsson, 2015).

The FBD process provides paleontologists with a far more realistic tree prior model than others previously available. For example, the FBD tree prior has recently been demonstrated to outperform a uniform prior (Matzke and Wright, 2016). Other
models, such as the Yule process or simple birth-death process are strongly violated when making phylogenetic inferences from paleontologic data. Moreover, the FBD tree prior has a high level of internal consistency for estimating age dates and a good fit to morphologic and geologic data in empirical, well-characterized data sets (e.g., penguins and canids, see Drummond and Stadler, 2016). Analyses of the crinoid data set herein assumed the simple case of constant rates for macroevolutionary and sampling parameters. However, the FBD process can be extended to a more sophisticated time-varying (i.e., piecewise-constant) model that may be useful for other data sets. Similarly, models could be developed to account for geographic variation in sampling probabilities (Wagner and Marcot, 2013). Such models may be especially beneficial for studies with larger, more comprehensive character matrices spanning similar to longer time intervals than considered herein (Gavryushkina et al., 2014; Zhang et al., 2016).

A major innovation of the FBD process as a tree prior is the ability to account for sampling ancestor-descendant relationships in phylogenetic analysis. Although the notion of discovering “true” ancestors is somewhat contentious (see Smith, 1994; Foote, 1996), modeling studies suggest ancestral morphotaxa are likely present in the fossil record of many paleontologically important groups (Foote, 1996). Gavryushkina et al. (2014) demonstrated that sampled ancestors should be accounted for when estimating phylogenies, even when ancestral morphotaxa are not of specific interest in the analysis, because not including them introduces biases in parameter estimation. Thus, even if sampled ancestors are considered nuisance parameters (Close et al., 2015; Gorscak and
O’Connor, 2016), they may nevertheless be important for accurately estimating more accurate tree topologies and node ages.

Parameter estimation under the FBD process does not require exhaustive sampling of fossil taxa, but it does require a representative random sample of species (e.g., the sampling strategy used herein) (Didier et al., 2012). However, the application of sampled-ancestor tip-dating methods to exhaustively sampled species-level (sensu Smith, 1994) or specimen-level data represents an important (but unexplored) frontier in phylogeny-based analyses of macroevolution. For example, coding multiple fossil specimens of species-level morphotaxa from different time horizons and/or geographic localities may provide a means for testing whether speciation events occur primarily through budding or bifurcating cladogenesis (Gavryushkina et al., 2014; Hunt and Slater, 2016). In addition, paleontologists are commonly interested in whether morphologic change is punctuated or gradual (Eldredge and Gould, 1972; Hunt, 2008). Testing alternative probabilistic models of character evolution within a similar phylogenetic and sampling framework as described above, where each model makes different assumptions about punctuated vs. gradual rates of change (as well as durations of stasis), would provide additional insight into the dynamics of morphologic evolution during speciation events (see Wagner and Marcot, 2010).

The emerging synthesis between paleontology and model-based phylogenetics contributes to the growing consensus that research programs in systematic paleontology are greatly enhanced when grounded in rigorous analytical approaches (Smith, 1994; Wagner, 2000a; Wagner and Marcot, 2010; Slater and Harmon, 2013; Hunt and Slater,
2016). Many of the analytical tools discussed in this paper were originally developed for non-paleontologic purposes. Thus, it is perhaps not surprising there is plenty of room for future modifications and refinement of these techniques to better test paleontologic patterns. Nevertheless, the development and application of these methods has already expanded our ability to quantitatively address macroevolutionary questions. Continued research implementing probabilistic approaches in phylogeny-based paleontology will likely return the favor and provide neontologists with evolutionary insights and unique perspectives only accessible to paleontologists.
Supplemental information: Calculating the probability density of FBD phylogenetic trees

This section provides equations for calculating the probability density of a sampled ancestor phylogenetic tree generated by the fossilized birth–death process. These trees are used as Bayesian priors for phylogenies (i.e., topology and divergence times) in the tip-dating analysis presented in the main text. The equations presented here follow Stadler (2010), Stadler et al. (2012), and Didier et al. (2012), with subsequent modifications by Gavryushkina et al. (2014). I encourage readers to refer to these references for additional details on birth-death-sampling models and their applications. Interested readers are also encouraged to see Gavryushkina et al. (2014) and Zhang et al. (2016) for a detailed description of a birth-death-sampling process with time heterogeneous (i.e., piecewise-constant) rates, as well as Bapst’s (2013) probabilistic method to a posteriori timescale un-dated cladograms. Please note that the notation used in this paper differs in places from that of the references mentioned above to be more consistent with the paleontological literature (e.g., Foote, 1997, 2000; Wagner and Marcot, 2010; Bapst, 2012).

For simplicity, ordered trees are used in the derivation below. However, ordered trees are subsequently modified to labeled trees (using a conversion factor) to calculate likelihoods (Stadler, 2010). Ordered trees distinguish between left and right branches and identify nodes via a unique left-right path from the root, whereas labeled trees instead give sampled nodes distinct labels to describe branching patterns and divergences.
(Stadler, 2010; Gavryushikina et al., 2014). Each labeled phylogenetic tree (Ψ) consists of two elements: a discrete, ranked tree topology Ψ and a continuous time vector τ. The ranked tree topology Ψ with ordered branching events is simply the branching pattern of common ancestry among \( m \) taxa distributed at the tips of the tree (i.e., an unscaled cladogram). The time vector τ assigns an unambiguous time to each node, such that it contains the following elements arranged in the exact descending temporal order in which they occur in the tree: the \( m - 1 \) lineage splitting times \((x_1, ..., x_{m-1})\), where \( x_{m-1} < ... < x_1 \); the \( m \) tip-taxon sampling times \((y_1, ..., y_m)\), where \( y_m < ... < y_1 \); and \( k \) sampling times of two-degree nodes \((z_1, ..., z_k)\) (Gavryushkina et al., 2014). The density of an ordered tree can be converted to a labeled tree by multiplying by the conversion factor \( \frac{2^n + m - 1}{n!(m + k)!} \) (see Stadler, 2010, p. 402).

To obtain the probability density of a given sampled ancestor phylogenetic tree (Ψ), the likelihood is calculated along each branch \( b \) in Ψ moving backward in time. The probability of any one event (i.e., branching with rate \( p \), extinction with rate \( q \), or sampling with rate \( r \)) occurring during a very small time step \( \Delta t \) is the product of its Poisson rate and \( \Delta t \). For example, the probability of a single branching event over a small time interval is \( p \Delta t \). The probabilities corresponding to any event happening more than once during \( \Delta t \) is summarized by an order term, \( O(\Delta t^2) \) (Feller, 1968). If \( \Delta t \) is chosen to be very small, then the probability of more than one event happening during the time interval can be ignored (see below). Because time is measured from the tips backward in time toward the root, each small time step \( \Delta t \) moves further into the past.
Let $\Psi_b(t)$ be the probability density that a lineage corresponding to branch $b$ at time $t$ produced the observed $\Psi$ between time $t$ and $t = 0$. Thus,

$$
\Psi_b(t_o) = f[\Psi | \pi = (p, q, r, \epsilon, t_o)].
$$

To obtain the probability density for $\Psi_b(t)$, I follow Stadler et al. (2012) and first consider describing $\Psi_b(t + \Delta t)$ and assume $\Psi_b(t)$ is known. After deriving an equation for how the probability density changes over a small time interval $\Delta t$, the definition of a derivative can be used to obtain a differential equation describing the change in probability toward the root. This differential equation is then integrated along branches to solve for $\Psi_b(t)$ across the phylogeny.

Consider the possible evolutionary histories for single lineage along $b$ from time $t$ to $\Delta t$ in the past. Moving down the branch, a lineage may either have undergone at least one branching event during $\Delta t$ or experienced no event at all (note that extinction is not considered here because a lineage cannot logically have gone extinct prior to its subsequent sampling). Thus, the equation for $\Psi_b(t + \Delta t)$ is

$$
\Psi_b(t + \Delta t) = (1 - (p + q + r)\Delta t - O(\Delta t^2)) \Psi_b(t) + p\Delta t 2S_0(t) \Psi_b(t) + O(\Delta t^2),
$$

(A1)

where $S_0(t)$ is the probability that a lineage at time $t$ has no sampled descendants (Stadler, 2010). The quantity $S_0(t)$ is given by Gavryushkina et al. (2014) as:
\[ S_0(t) = \frac{p + q + r + c_1 e^{-c_1 (1 - c_2)} - (1 + c_2)}{2p} \]

where

\[ c_1 = \sqrt{(p + q + r)^2 + 4pr} \] and \[ c_2 = \frac{p - q - 2p\varepsilon - r}{c_1} \].

The logic behind Equation A1 is straightforward to interpret if each term on the right hand side is considered in isolation. The first term, \( (1 - (p + q + r)\Delta t - O(\Delta t^2)) \), is the probability that no event takes place along \( b \) during \( \Delta t \). The second term reflects the probability of lineage splitting, where \( p\Delta t \) is the probability that one branching event takes place and \( 2S_0(t) \) accounts for the probability that one of the two descendant lineages (either the left or right descendant) left no sampled descendants in the observed tree. The final term, \( O(\Delta t^2) \), is a summary term corresponding to the probabilities for multiple events during \( \Delta t \).

Now that we have an expression for \( \Psi_b(t + \Delta t) \), if we modify Equation A1 to consider how the probability density changes from time \( t \) to time \( t + \Delta t \), we get:

\[ \frac{\Psi_b(t + \Delta t) - \Psi_b(t)}{\Delta t} = - (p + q + r)\Psi_b(t) + 2pS_0(t)\Psi_b(t) + O(\Delta t). \]

Finally, taking the limit as \( \Delta t \to 0 \) results in the differential equation:
\[
\frac{d}{dt} \Psi_b(t) = - (p + q + r) \Psi_b(t) + 2pS_0(t) \Psi_b(t).
\]

(A2)

Letting \( T_e \) represent the terminal end of a branch \( b \), then the initial values at \( t = T_e \) are:

\[
\Psi_b(T_e) = \begin{cases} 
p \Psi_{b1}(T_e) \Psi_{b2}(T_e) & \text{if } b \text{ has two descendant branches, } b_1 \text{ and } b_2 \\
r \Psi_{b1}(T_e) & \text{if } b \text{ has one descendant branch } b_1 \\
rS_0(T_e) & \text{if } b \text{ has no descendant branches and } T_e > 0 \\
\epsilon & \text{if } b \text{ has no descendant branches and } T_e = 0.
\end{cases}
\]

Conditioning on the clade’s origin (i.e., the age of the root) and the event \( S_\epsilon \), where \( S_\epsilon \) denotes that at least one lineage was sampled at the end of the process, the closed form solution for the probability density of \( \Psi \) accounting for labeled trees is (Stadler, 2010, p. 400; Gavryushkina et al., 2014, equation 3):

\[
\Psi_b(t_o) = f \left[ \Psi \mid \pi = (p, q, r, \epsilon, t_o, S_\epsilon) \right] = \frac{1}{(m + k)! \left( p(1 - \hat{S}_o(t_o))^2 \right)} r^k \epsilon^n \varphi(t_o) \prod_{i=1}^{m+n-1} 2p\varphi(x_i) \prod_{i=1}^{m} rS_0(y_i)\varphi(y_i)^{-1},
\]

(A3)

where \( n \) is the number of \( \epsilon \) sampled lineages, \( S_0 \), \( c_1 \), and \( c_2 \) are defined as above, with

\[
\varphi(x) = \frac{4}{2(1 - c_2^2) + e^{c_1x}(1 - c_2^2) + e^{c_1x}(1 + c_2)^2},
\]

and
\[
\hat{S}_0(t_o) = 1 - \frac{\varepsilon(p - q)}{p\varepsilon + (p(1 - \varepsilon) - q)\varepsilon^{-\varepsilon(p-q)t}}.
\]

**Accessibility of supplemental data**

Supplemental data deposited in Dryad data package

http://datadryad.org/resource/doi:10.5061/dryad.6hb7j
References


Bapst, D.W., and Hopkins, M.J., in press, Comparing cal3 and other a posteriori time-scaling approaches in a case study with the Pterocephaliid trilobites: Paleobiology.


Hall, J., 1852, Palaeontology of New York, v. 2, Containing descriptions of the organic remains of the lower middle division of the New-York system. Natural History of New York,


Hunt, G., 2008, Gradual or pulsed evolution: when should punctuational explanations be preferred?: Paleobiology, v. 34, p.360–377.


Lane, N.G., 1970, Lower and Middle Ordovician crinoids from west-central Utah: Brigham Young University Geology Studies, v. 17, p. 3–17.


Moore, R.C., and Teichert, C., eds., 1978, Treatise on Invertebrate Paleontology, Part T, Echinodermata 2: Geological Society of America and University of Kansas Press, Lawrence, Kansas, 1027 p.


Slater, G.J., 2013, Phylogenetic evidence for a shift in the mode of mammalian body size evolution at the Cretaceous-Palaeogene boundary: Methods in Ecology and Evolution, v. 4, p. 734–744.


Table 3.1 Species sampled for phylogenetic analysis.
<table>
<thead>
<tr>
<th>Species</th>
<th>Author</th>
</tr>
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<tbody>
<tr>
<td><em>Aethocrinus moorei</em></td>
<td>Ubaghs, 1969</td>
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<tr>
<td><em>Alphacrinus mansfieldi</em></td>
<td>Guensburg, 2010</td>
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<td></td>
<td>Webster, Maples, Mawson, and Dastanpour, 2003</td>
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<tr>
<td><em>Amabilicrinus iranensis</em></td>
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<td><em>Apktocrinus ubaghsi</em></td>
<td>Guensburg and Sprinkle, 2009</td>
</tr>
<tr>
<td><em>Botryocrinus ramosissimus</em></td>
<td>Angelin, 1878</td>
</tr>
<tr>
<td><em>Carabocrinus radiatus</em></td>
<td>Billings, 1857</td>
</tr>
<tr>
<td><em>Codiocrinus granulatus</em></td>
<td>Schultze, 1867</td>
</tr>
<tr>
<td><em>Colpodecrinus quadrifidus</em></td>
<td>Sprinkle and Kolata, 1982</td>
</tr>
<tr>
<td><em>Corematocrinus plumosus</em></td>
<td>Goldring, 1923</td>
</tr>
<tr>
<td><em>Crotalocrinites verucosus</em></td>
<td>(Schlotheim, 1820)</td>
</tr>
<tr>
<td><em>Cupulocrinus humilis</em></td>
<td>(Billings, 1857)</td>
</tr>
<tr>
<td><em>Dendrocrinus longidactylus</em></td>
<td>Hall, 1852</td>
</tr>
<tr>
<td><em>Euspirocrinus spiralis</em></td>
<td>Angelin, 1878</td>
</tr>
<tr>
<td><em>Eustenocrinus springeri</em></td>
<td>Ulrich, 1925</td>
</tr>
<tr>
<td><em>Gasterocoma antiqua</em></td>
<td>Goldfuss, 1839</td>
</tr>
<tr>
<td><em>Glossocrinus naplesensis</em></td>
<td>Goldring, 1923</td>
</tr>
<tr>
<td><em>Heviocrinus melendezi</em></td>
<td>Gil Cid, Alonso, and Pobes, 1996</td>
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<tr>
<td><em>Homalocrinus nanus</em></td>
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<td><em>Hybocrinus conicus</em></td>
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<td><em>Hybocystites problematicus</em></td>
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<tr>
<td><em>Ibexocrinus lepton</em></td>
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<tr>
<td><em>Ichthyocrinus laevis</em></td>
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<tr>
<td><em>Iocrinus subcrassus</em></td>
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<td><em>Lecanocrinus macropetalus</em></td>
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<td><em>Lecythocrinus eifelianus</em></td>
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<td><em>Manicrinus hybocriniformis</em></td>
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<td><em>Mastigocrinus arboreus</em></td>
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<td><em>Merocrinus typus</em></td>
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<td><em>Metabolocrinus rossicus</em></td>
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<td><em>Ottawacrinus typus</em></td>
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<td><em>Petalocrinus mirabilis</em></td>
<td>Weller and Davidson, 1896</td>
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<td><em>Plicodendrocrinus casei</em></td>
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<td><em>Porocrinus conicus</em></td>
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<td><em>Proctothylacocrinus longus</em></td>
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Continued
Table 3.1 continued

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<td>Protaxocrinusovalis</td>
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<td>Rhenocrinus ramoissimus</td>
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<td>Rutkowskicrinus patriciae</td>
<td>McIntosh, 2001</td>
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<td>Sagenocrinites expansus</td>
<td>(Phillips, 1839)</td>
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<td>Sphaerocrinus geometricus</td>
<td>(Goldfuss, 1831)</td>
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<td>Streblocrinus brachiatus</td>
<td>Koenig and Meyer, 1965</td>
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<tr>
<td>Thalamocrinus ovatus</td>
<td>Miller and Gurley, 1895</td>
</tr>
<tr>
<td>Thenarocrinus callipygus</td>
<td>Bather, 1890</td>
</tr>
</tbody>
</table>
Figure 3.1 Illustration of the fossilized birth–death process. (1) A full realization of the FBD process from time $t$ in the past to the end of the process. Diversification produces a tree with branching and extinction events and random sampling of nodes. Sampling events are indicated by dots. (2) A “reconstructed” phylogenetic produced by pruning all of the unsampled lineages in 1.1. Thus, only the observed portion of samples participating in the macroevolutionary process is observed. Note that some sampled nodes represent ancestors.
Fig. 3.1
Figure 3.2 Parsimony-based estimate of rate variation among characters. This distribution suggests that many characters evolve slowly, whereas a small number of characters evolve at much higher rates.
Fig. 3.2
Figure 3.3 Testing statistical associations between the amount of morphologic evolution inferred from an undated analysis and divergence times estimated under a relaxed morphologic-clock model: (1) node age in millions of years and anagenesis (measured as the total root-to-tip distance in parsimony steps from an undated analysis), (2) phylogenetic independent contrasts between branch durations (from time-scaled analysis) and anagenesis (from an undated analysis). Both regressions are statistically significant.
Fig. 3.3

1. Anagenesis (root to tip distance) vs. Age (million yrs ago)

2. PIC (Anagenesis) vs. PIC (branch duration)

$P = 0.017$

$P = 0.005$
Figure 3.4 Maximum Clade Credibility tree of early to middle Paleozoic crinoids.

Posterior probabilities (> 0.50) are located next to nodes and expressed in percent, blue node bars represent the 95% highest posterior density age estimates, thick black bars represent genus-level stratigraphic ranges. Note the inclusion of stratigraphic ranges give the appearance of sister taxon relationships where zero-length branches were sampled (e.g., *Cupulocrinus*). The Cladida (sensu Simms and Sevastopulo, 1993) are sister to the Disparida. Crinoid taxa depicted represent the major clades discussed in the text: (from top to bottom), the disparid *Eustenocrinus springeri* Ulrich, 1925, redrawn from Ubaghs (1978); representative porocrinoid and hybocrinid (see text), *Hybocrinus conicus* Billings, 1857, redrawn from Sprinkle and Moore (1978); the flexible *Protaxocrinus laevis* (Billings, 1857), redrawn from Springer (1911); representative eucladid *Dictenocrinus*, redrawn from Bather (1900).
Fig. 3.4
Chapter 4: Phylogenetic taxonomy and classification of the Crinoidea (Echinodermata)

Abstract.—A major goal of biological classification is to provide a system that conveys phylogenetic relationships while facilitating lucid communication among researchers. Phylogenetic taxonomy is a useful framework for defining clades and delineating their taxonomic content based on well-supported phylogenetic hypotheses. The Crinoidea (Echinodermata) is one of the five major clades of living echinoderms and has a rich fossil record spanning nearly a half billion years. Using principles of phylogenetic taxonomy and recent phylogenetic analyses, we provide the first phylogeny-based definition for the Clade Crinoidea and its constituent subclades. A series of stem- and node-based definitions are provided for all major taxa traditionally recognized within the Crinoidea, including the Camerata, Disparida, Hybocrinida, Cladida, Flexibilia, and the Articulata. Following recommendations proposed in recent revisions, we recognize several new clades, including the Eucamerata Cole (in press), Porocrinoidea Wright (in press), and Eucladida Wright (in press). In addition, recent phylogenetic analyses support the resurrection of two names previously abandoned in the crinoid taxonomic literature: the Pentacrinoidea Jaekel, 1918 and Inadunata Wachsmuth and Springer, 1885. Lastly, a phylogenetic perspective is used to inform a comprehensive revision of the traditional rank-based classification. Although an attempt was made to minimize changes to the rank-based system, numerous changes were necessary in some cases to achieve
monophyly. These phylogeny-based classifications provide a useful template for paleontologists, biologists, and non-experts alike to better explore evolutionary patterns and processes with fossil and living crinoids.

**Introduction**

Crinoids are a diverse, long-lived clade of echinoderms with a fossil record spanning nearly half a billion years and are represented by more than 600 species living in marine ecosystems today (Hess et al., 1999). The geologic history of crinoids is revealed through a highly complete, well-sampled fossil record (Foote and Raup, 1996; Foote and Sepkoski, 1999) displaying a complex pageant of evolutionary radiation, extinction, ecologic innovation, and morphologic diversification (Ausich and Bottjer, 1982; Ausich et al., 1994; Foote, 1999; Peters and Ausich, 2008; Deline and Ausich, 2011; Gorzelak et al, 2015). The spectacular fossil record of crinoids is greatly enriched and complemented by detailed biologic studies on living species. These studies facilitate opportunities to synthesize information from fossil and extant forms. For example, comparative studies between fossil and living crinoid species have provided insight into species ecology and niche dynamics (Meyer and Macurda, 1977; Ausich, 1980; Roux, 1987; Kitazawa et al., 2007; Baumiller 2008), established developmental bases for morphologic homologies (Shibata et al., 2008; Wright, 2015a), and informed phylogenetic hypotheses (Simms and
Sevastopulo, 1993; Rouse et al., 2013). Thus, crinoids form a data-rich model system for exploring major questions in the history of life.

Given their general significance and broad scientific utility across multiple disciplines of inquiry, it is paramount that the biological classifications of crinoids reflect their evolutionary heritage. Numerous emendations and informal suggestions for major taxonomic revisions have been opined over the last few decades (e.g., Kelly, 1986; Simms and Sevastopulo, 1993; Ausich, 1998a, 1998b; Webster and Jell, 1999; Hess and Messing, 2011), but the most recent comprehensive revision to crinoid classification is the 1978 *Treatise on Invertebrate Paleontology* (Moore and Teichert, 1978). Since publication of the *Treatise*, the value of revising rank-based systematic classifications to be consistent with phylogenetic hypotheses and/or the explicit use of phylogenetic taxonomy (*sensu* de Quieroz and Gauthier, 1990; Sereno, 1999, 2005) has become increasingly common in paleontology (e.g., Smith, 1984, 1994; Holtz, 1996, 1998; Sereno, 1997; Padian et al., 1999; Brochu and Sumrall, 2001; Carlson, 2001; Carlson and Leighton, 2001; Brochu, 2003; Forey et al., 2004; Sereno et al., 2005; Butler et al., 2008; Kelley et al., 2013). We agree with these authors that all named taxa in a biological classification system should ideally represent clades (i.e., monophyletic groups). The development of phylogeny-based classifications is not without difficulties or criticism (e.g., Benton, 2000; 2007). However, we advocate that recent advances in understanding the phylogenetic relationships of major crinoid lineages make the biological classification of the Crinoidea ripe for revision.
A great strength of so-called “phylogenetic taxonomy” is its potential for increasing nomenclatural stability (de Quieroz and Gauthier, 1994; Brochu and Sumrall, 2001). Under a phylogeny-based system of classification, groups of taxa are organized by their patterns of shared common ancestry rather than diagnostic traits. This is a particularly useful aspect of phylogenetic taxonomy: if named evolutionary units are defined by their history of common ancestry, they do not change if new information comes to light that necessitates modification of taxonomic diagnoses. For example, new fossil discoveries and/or more nuanced understandings of phylogenetic relationships may alter the distribution of synapomorphies among members of a clade but do not alter the definition of the clade. Moreover, by naming taxa based on cladogram topologies, phylogenetic taxonomy can provide a precise definition for groups previously difficult to diagnose by a unique combination of synapomorphies, such as the Articulata (Simms, 1988; Webster and Jell, 1999; Rouse et al., 2013). To avoid potential instability in taxonomic nomenclature and/or the proliferation of clade names, we advocate that major changes in crinoid systematics should (1) be based on well-supported phylogenetic hypotheses inferred using rigorous and repeatable quantitative techniques and (2) employ widely used names and/or names with historical precedence if available.

In this paper, we propose a series of stem-based and node-based clade definitions to help standardize nomenclature for crinoid higher taxa. The clade definitions proposed herein are informed by a series of recent phylogenetic analyses (Ausich et al., 2015; Cole, in press; Wright, in press) and represent the first attempt to classify crinoids using the principles of phylogenetic taxonomy (de Queiroz and Gauthier 1992, 1994).
Although Linnaean classifications lack rigorous criteria for assigning ranks, they can nevertheless provide useful (if coarse) reflections of phylogenetic relatedness and divergence among taxa, particularly in paleontology (Smith, 1984; Potter and Freudenstein, 2005; Jablonski and Finarelli, 2009; Soul and Friedman, 2015). Given the widespread use of rank-based classifications among invertebrate paleontologists in both alpha taxonomy and paleobiological studies, it is prudent to present a phylogenetically informed revision of the rank-based classification of the Crinoidea. These revisions modify the existing Linnaean classification of crinoids to better represent the set of nested hierarchies implied by phylogenetic trees (Ausich et al., 2015; Cole, in press; Wright, in press).

In their review of progress made in crinoid research during the 20th century, Ausich and Kammer (2001, p. 1167) stated the “immediate challenge for the [21st century] study of crinoids is to establish a phylogenetic classification for the entire class.” It is our hope that the dual classification systems presented herein will provide a foundation for future studies employing phylogenetic nomenclature in crinoid research and also promote the use of an improved classification system among researchers who choose to work with the Linnaean system.
The dredge and the hammer: a brief history of crinoid classification

“The whole history of the attempts to classify the Crinoidea shows...the gradual emancipation from the older habit of lumping forms together because they are alike in structure without considering how the likeness arose” –F.A. Bather (1898, p. 339)

Formal scientific description and classification of crinoids began in 1821 when J.S. Miller recognized fossilized stalked echinoderms from the “environs of Bristol” as a distinct group. Although he did not include comatulids in his original conception of the Crinoidea, he anticipated that they were crinoids: “The combination of these results with those from the Crinoidea made me anxious to examine the Comatulae...an animal which would be defined with sufficient precision as a Pentacrinus destitute of the column (Miller, 1821, p. 127).” Further, he judged Marsupites ornatus Miller, 1821 (an unstalked crinoid of Cretaceous age) to be the “link” between comatulids and his Crinoidea (Miller, 1821, p. 139). Extant stalked crinoids were unknown until the mid- to late 1860s, when their discovery during oceanic dredging expeditions provided fodder for early debates regarding the efficacy of Darwin’s (1859) then recently proposed theory of natural selection (see Alaniz, 2014; Etter and Hess, 2015). Thus, the original description, definition, and diagnosis of the Crinoidea relied entirely on fossil remains. Despite the morphological diversity and deep phylogenetic relationships among groups of extant species, the inclusion of living crinoids with fossil forms has not fundamentally altered Miller’s (1821) concept. Following subsequent inclusion of the comatulids and extant
stalked crinoids with fossil forms, the Crinoidea has withstood nearly 200 years of scrutiny as a distinct group within the Echinodermata.

In contrast with their long-term recognition as a clade, the classification of taxa within the Crinoidea has been widely debated since the 19th century (Müller, 1841; Angelin, 1878; Wachsmuth and Springer, 1897; Bather, 1899; Springer, 1913; Jaekel, 1918). With few exceptions, debates on crinoid classification have primarily been based on disagreements over phylogenetic affinities among taxa rather than systematic practices among researchers (see Bather, 1899 for a counter example). The intensity of early debates over crinoid classification is best epitomized by the frequent yet acrimonious exchanges between Wachsmuth and Springer (e.g., 1885, 1891, 1897) and Bather (e.g., 1898, 1899, 1900). Attempts to resolve these debates among 19th century systematists have largely shaped the last ~70 years of crinoid research (Ausich and Kammer, 2001).

In their seminal work *Evolution and Classification of Paleozoic Crinoids*, Moore and Laudon (1943) presented a classification that incorporated aspects of both Frank Springer’s and Francis Bather’s ideas (see discussion in Ausich and Kammer, 2001). With few modifications, Moore and Laudon’s (1943) publication formed the basis for the *Treatise on Invertebrate Paleontology* (Moore and Teichert, 1978). Following publication of the 1978 *Treatise*, the classification of crinoids entered a protracted yet frail era of nomenclatural stability. Although few authors have advanced major revisions or comprehensive modifications, many have voiced contention with the *Treatise* classification (Kelly, 1982, 1986; Kolata, 1982; McIntosh, 1984, 1986, 2001; Ausich, 1986, 1998a, 1998b; Donovan, 1988; Simms, 1988; Simms and Sevastopulo, 1993;
Brower, 1995; Webster and Jell, 1999; Guensburg and Sprinkle, 2003; Hess and Messing, 2011; Guensburg, 2012; Ausich et al., 2015). With the exception of Simms and Sevastopulo (1993), all of these studies have basically been readjustments of the Moore and Teichert (1978) classification to accommodate rank changes, the addition of new groups, and delineation of clade membership defined by phylogenetic studies of extant species.

The study of extant crinoids remains in the shadow of A. H. Clark, who published more than 100 publications on their morphology, taxonomy, and classification during the early to middle 20th century (e.g., A. H. Clark, 1915, 1921; A. H. Clark and A. M. Clark, 1967). The advent and application of molecular phylogenetic methods to crinoid phylogeny has recently thrown light on relationships among extant species (Cohen et al., 2004; Hemery et al., 2013; Rouse et al., 2013; Summers et al., 2014). However, these analyses also point toward the need for extensive taxonomic revisions and an improved understanding of morphologic traits among living species (Messing and White, 2001; David et al., 2006; Roux et al., 2013; Summers et al., 2014; Hays et al., 2015). Remarkably, there has been little previous work to combine molecular phylogenetic studies of extant crinoids with paleontologic data to assemble a more complete picture of post-Paleozoic crinoid evolutionary history. Efforts to integrate these rich sources of information present both challenges and opportunities for future researchers to resolve patterns and processes shaping the crinoid tree of life (Lee and Palci, 2015; Pyron, 2015).
Crinoid origins and classification

Extant echinoderms include the Crinoidea, Echinoidea, Ophiuroidea, Asteroidea, and the Holothuroidea, with the latter four comprising the Eleutherozoa. Although it has been long established that crinoids form the sister group to the Eleutherozoa, the relationships among many fossil and extant echinoderm groups are controversial (Paul and Smith, 1984; Sumrall 1997; David et al., 2000; Smith, 2005; Pisani et al., 2012; Telford et al., 2014; Zamora and Rahman, 2014; Feuda and Smith, 2015; Reich et al., 2015). The phylogenetic position of crinoids within the Echinodermata was contested throughout the late 20th century, with a focal question whether the Pelmatozoa (i.e., stalked echinoderms including blastozoans and crinoids) and/or the Blastozoa are monophyletic groups or a “grade” of body plan organization. This is a fundamental question not only for understanding the origin of crinoids but also for resolving phylogenetic relationships among clades within the Echinodermata. One hypothesis of crinoid origins postulates that crinoids and blastozoan echinoderms independently evolved pelmatozoan-grade body plans (e.g., Sprinkle, 1973, 1976; Mooi and David, 1998, 2008; Guensburg and Sprinkle, 2003; David et al., 2000; Guensburg, 2012). This hypothesis proposes that blastozoans and crinoids each comprise distinct monophyletic groups. In contrast, an alternative hypothesis postulates that blastozoans and crinoids are members of an inclusive pelmatozoan clade, with crinoids nested within a paraphyletic Blastozoa (Leuckart, 1848; Bather, 1899, 1900; Smith, 1984; Paul and Smith, 1984; Paul, 1988; Smith and Jell, 1990; Smith, 1994; Sumrall, 1997; Ausich, 1998a, 1998b; Clausen et al., 2009; Zamora
and Smith, 2011; Kammer et al., 2013; O’Malley, 2016). In this hypothesis, the blastozoan body plan represents a grade of organization within the more inclusive Pelmatozoa, a clade comprising all blastozoan grade echinoderms and crinoids (including the crown group). Although the inclusive group of nominal ‘blastozoan’ taxa is not monophyletic, there are undoubtedly assemblages of ‘blastozoan’ taxa that do correspond to monophyletic groups (Smith, 1984; Sumrall and Wray, 2007; Zamora and Smith, 2011; Sumrall and Waters, 2012; Zamora et al., 2016).

Important to this debate are the differences among researchers with respect to their underlying taxonomic principles and systematic practices (see Smith, 1988). Those who support the monophyly of the Blastozoa and Crinoidea embrace systematic practices that emphasize differences (rather than similarities) among taxa, recognize plesiomorphic traits as taxonomically informative characters, exclude character data from consideration of relationships because of a priori beliefs regarding the distribution of homoplastic traits, and conflate sister group hypotheses with ancestor-descendant relationships (e.g., Guensburg and Sprinkle, 2003, 2007; Guensburg, 2012; Guensburg et al., 2016). These practices differ considerably from those who infer the Pelmatozoa as a clade. These workers tend to emphasize similarities (rather than differences) among taxa, minimize a priori assumptions regarding hypotheses of character evolution, and utilize the principles of phylogenetic systematics to rigorously test whether apparent similarities in form reflect synapomorphies or homoplasy (e.g., Sumrall and Waters, 2012; Sumrall, 2014; Ausich et al., 2015). Given the recent advances in homology assessment among pentaradiate echinoderms (e.g., Sumrall, 1997, 2008, 2010, 2014; Sumrall and Waters,
2012; Kammer et al., 2013) and computational phylogenetic analyses of echinoderm taxa based on a large ensemble of characters, it is becoming increasingly clear that a blastozoan-grade taxon likely forms the closest immediate outgroup to the Crinoidea (Kammer et al., 2013; Sumrall, 2014). In the future, new developments in phylogenetic research along with a continued search for the oldest “crinoid” fossils will continue to play a role in uncovering the sequence of morphologic transitions behind the assembly of the crinoid body plan.

Despite desultory disagreements regarding crinoid origins (Sprinkle, 1973; Ubags, 1978; Donovan, 1988; Ausich, 1998a, 1998b; Ausich and Babcock, 1998; Guensburg and Sprinkle, 2007, 2009; Kammer et al., 2013; Guensburg, 2012; Ausich et al., 2015; Guensburg et al., 2016), there is nevertheless considerable agreement among workers regarding the pattern of branching relationships within the crinoid ingroup. For example, the recent phylogenetic analyses of Guensburg (2012) and Ausich et al. (2015) reveal highly congruent patterns of branching relationships among crinoid higher taxa despite the use of alternative outgroups, different datasets, and alternative interpretations of homologous morphologic characters. We surmise this growing consensus stems from the improved taxonomic sampling of the oldest known crinoids (Guensburg and Sprinkle, 2003, 2009; Guensburg, 2010) and implementation of more rigorous quantitative approaches to testing phylogenetic hypotheses (Guensburg, 2012; Ausich et al., 2015; Cole, in press; Wright, in press).

We conclude that congruence observed among tree topologies obtained from researchers with different perspectives indicates strong support for these patterns.
Although questions surrounding crinoid origins remain, this debate is moot with respect to the phylogeny-based definitions and classification presented herein and ultimately has no bearing on the focus and conclusions of this paper.

**Toward a phylogenetic classification of the Crinoidea**

From the perspective of their geologic history, crinoids are a bottom-heavy clade (Gould et al., 1987). In contrast to the tremendously diverse assemblage of stem lineages, comparatively few species are encompassed within the crown group (Fig. 4.1). Because of the enormous diversity of the stem group relative to the crown group, fossil crinoids have received much systematic attention compared to their extant representatives (but see A. H. Clark, 1915; David et al., 2006; Hess and Messing, 2011; Rouse et al., 2013; Hemery et al., 2013). Aside from a number of smaller studies examining relationships among species of middle to late Paleozoic genera (e.g., Ausich and Kammer, 2008; Gahn and Kammer, 2002; Kammer and Gahn, 2003), most investigations of crinoid phylogeny have focused on discerning relationships among Ordovician taxa (Brower, 1995; Ausich 1998b; Guensburg 2012; Ausich et al. 2015; Cole, in press). The Ordovician Period represents a key interval in crinoid evolution because species belonging to various groups of traditionally named taxa first appear in rocks of the Lower Ordovician (Tremadocian) (Guensburg and Sprinkle, 2003, 2009; Guensburg, 2010) and the majority of well-studied groups had originated prior to its close.
The divergence between camerate and non-camerate lineages forms a fundamental, early split in the history of crinoid evolution (Jaekel, 1918; Donovan, 1988; Guensburg, 2012; Ausich et al., 2015; Cole in press; Wright, in press) (Fig. 1). For example, in the recent phylogeny of Ausich et al. (2015), taxa belonging to the Camerata (*sensu* Moore and Teichert, 1978) form the sister clade to all other crinoids, including the protocrinoids (Guensburg and Sprinkle, 2003). Disparids were recovered as sister to a clade comprised of most ‘cladid’ taxa and hybocrinids were recovered as sister to a group of ‘cyathocrine’ cladids (*sensu* Moore and Teichert, 1978). A similar pattern was recovered by Guensburg (2012, fig. 2).

Building on these studies, Cole (in press) further assessed the basal split between camerates and non-camerates and tested the taxonomic status of the Monobathrida and Diplobathrida (Fig. 1). Wright’s (in press) analysis of relationships among non-camerate crinoids offers a more nuanced perspective of this portion of the crinoid tree than previously recovered. Notably, many so-called Ordovician “clades” of Guensburg (2012) and Ausich et al. (2015) do not retain their status of monophyly when post-Ordovician taxa are considered (Wright, in press).

Recent molecular phylogenetic studies indicate broad relationships among major clades of extant crinoids are also reaching a consensus, with the Isocrinida representing the sister clade to all other extant crinoids (Rouse et al., 2013, 2015). Interestingly, divergence time estimation based on relaxed molecular clock models suggests the split between isocrinids and other extant groups took place some 231–252 million years ago.
(Rouse et al., 2013). Thus, molecular phylogenetic analyses and paleontological evidence are in general agreement regarding an ancient origin of the crinoid crown group.

A summary tree based on results presented in Ausich et al. (2015), Cole (in press), Wright (in press), and Rouse et al. (2013) is depicted in the form of a simplified cladogram in Figure 4.2. This cladogram is annotated with the clade names we propose below. Terminal taxa in the cladogram were carefully chosen to maximize stability in phylogenetic nomenclature (Table 3.1). Sereno (2005) listed numerous criteria for choosing the taxon specifiers in clade definitions. These recommendations include choosing specifiers that are nested rather than basal (if possible), represented by well-known or readily available material, and using multiple specifiers where necessary to accommodate phylogenetic uncertainty and/or alternative hypotheses. We have carefully chosen our clade definitions to not hinge on labile phylogenetic hypotheses or specific interpretations of unusual and/or problematic taxa.

Classes of clade definitions used in phylogenetic taxonomy and their graphical representations used herein closely follow Sereno (1999, 2005). Node-based clade definitions circumscribe the most recent common ancestor of at least two taxa and all of its descendants. Thus, node-based definitions form the least inclusive clade containing a minimum of two specifiers. In contrast, stem-based definitions circumscribe the most inclusive clade containing at least one internal specifier. In both cases, additional precision is obtained by identifying external specifiers falling outside the clade (i.e., the outgroup). For example, a stem-based definition for hypothetical Clade A with two internal and one external taxon specifiers can be stated as “all species sharing a more
recent common ancestor with species $X$ and $Y$ than $Z'$, where $X$ and $Y$ are internal taxon specifiers and $Z$ is an external specifier. In other words, Clade $A$ is stem-defined as the most inclusive clade containing $X$ and $Y$ but not $Z$. Note the presence of one species as an external specifier effectively eliminates the entire clade to which it belongs. By definition, a clade cannot contain an ancestor of its sister group.

In phylogenetic taxonomy, clade membership is not determined by the presence or absence of a “key” morphologic feature unless that apomorphy (or set of apomorphies) is listed in the definition as a qualifying clause (Sereno, 2005). We avoid apomorphic qualifiers in our definitions for several reasons. First, incomplete preservation may lead to cases where it is unknown whether a fossil species has the “key” feature diagnostic of the clade in question. Thus, the inclusion or exclusion of a fossil species depends on character state optimizations rather than direct data. Second, a trait may be “absent” in a taxon either because it was truly absent or because it was secondarily lost. Similarly, a trait may be “present” because of convergent evolution. Moreover, stem group taxa commonly have highly heterogeneous distributions of apomorphic traits, which may lead to instability when new taxa are sampled and/or alternative topologies are equally likely. Lastly, the timing of a divergence event may not correspond with the acquisition of a diagnostic apomorphy. For example, the blastozoan $Macrocystella$ is widely recognized as a basal glyptocystitoid rhombiferan even though it lacks the respiratory structures traditionally “diagnostic” of the Glyptocystida (Paul, 1968; Sprinkle, 1973; Zamora et al., 2016). All of these considerations are highly important when considering patterns of
character evolution but may lead to nomenclatural instability if incorporated into clade definitions.

Although we avoid the use of apomorphies to define clades, we do discuss morphological traits potentially useful for taxonomic diagnoses. In some cases, our proposed clade definitions retain much of their traditional meaning and taxonomic content, with constituent taxa sharing numerous synapomorphies that form unambiguous taxonomic boundaries (e.g., the Flexibilia). However, in other cases, either substantial revision was necessary and/or a list of unambiguous diagnostic characters were difficult or impossible to obtain (e.g., the Articulata). These challenges highlight the utility of phylogenetic taxonomy. For example, many authors have remarked that the Articulata has lacked a concise, unambiguous definition since it was first erected by J. S. Miller nearly 200 years ago (Simms, 1988; Webster and Jell, 1999; Hess and Messing, 2011; Rouse et al., 2013). A phylogenetic definition of the Articulata provides a clearer criterion for clade membership and results in a framework for future phylogenetic research assessing relationships among hypothesized stem clades, crown group synapomorphies, and subsequent morphologic transitions among crown group subclades.

The clade definitions and revised classification proposed herein represent the present state of knowledge, but systematics is a dynamic science and taxonomic theories are commonly reinterpreted in light of new discoveries. We fully expect our definitions to be refined and/or modified as more information becomes available. Some places of the crinoid tree still require extensive taxonomic revisions, such as Upper Paleozoic ‘cladids’ (sensu Moore and Laudon, 1943) and stem articulates (Wright, 2015b). Despite these
potential vicissitudes in the taxonomic content and/or definitions within our proposed classification, we agree with G.G. Simpson’s sentiment: “It is pusillanimous to avoid making our best efforts today because they may appear inadequate tomorrow” (1944, p. xxx [sic]).

**Systematic paleontology**

Crinoidea Miller, 1821


*Remarks.*—This definition captures J. S. Miller’s (1821) original concept based on fossil specimens and retains the name Crinoidea as the clade comprising the crown group plus all extinct species sharing a more recent common ancestor with a living crinoid than any echinoderm taxon listed above as external specifiers (Fig. 4.2). Further, this definition...
closely resembles the traditional use and taxonomic content of the Crinoidea as used by both biologists and paleontologists (Bather, 1899; Clark, 1915; Jaekel, 1918; Moore and Teichert, 1978; Hess et al., 1999; Rouse et al., 2013) and accommodates the current state of uncertainty regarding their nearest extinct sister group. In the interest of preserving the taxonomic content and common meaning of a widely used name, our Clade Crinoidea is preferred over Sumrall’s (1997) similarly defined Crinoideaformes (see Cantino and de Queiroz, 2010, p. 42). The Crinoidea is comprised of two major clades, the Camerata and the Pentacrinoidea, reflecting the early divergence between camerate and non-camerate crinoids (Jaekel, 1918; Donovan, 1988; Guensburg, 2012; Ausich et al., 2015). Because we provide the Crinoidea with a stem-based definition, the discovery of stemward fossils is accommodated within this definition.

Internal taxon specifiers were chosen because they were included in J. S. Miller’s (1821) original description and represent well known, well preserved, and highly-nested members of their respective subclades. In contrast to the internal taxon specifiers, the choice of external specifiers is more complex. The use of external specifiers in this definition spanning various ‘blastozoan’ and edrioasteroid-grade groups reflects the current difficulty involved in postulating the nearest definitive sister group as well as the uncertain state of relationships among extinct stemmed echinoderms (Smith, 1984; Sumrall, 1997, 2014; Ausich, 1998a, 1998b; Guensburg and Sprinkle, 2009; Kammer et al., 2013; Ausich et al., 2015; O’Malley et al., 2016; Guensburg et al., 2016).

Ausich et al.’s (2015) analysis of Ordovician crinoids took a conservative approach to outgroup selection by sampling broadly across taxa nested within the Clade
Pelmatozoa (Kammer et al., 2013; Sumrall, 2014). Similarly, we have chosen species from multiple pelmatozoan groups as external specifiers to help provide nomenclatural stability in the presence of phylogenetic uncertainty. Other taxa hypothesized to represent the crinoid sister group include the stylophorans (David et al., 2000) and edrioasteroids (Guensburg and Sprinkle, 2009; Guensburg et al., 2016). Stylophorans have long been considered non-radiate stem group echinoderms (e.g., Paul and Smith, 1984; Smith, 1984; Smith, 2008) and have been cogently demonstrated to lack crown group synapomorphies (Smith, 2005). Thus, we do not consider the stylophoran hypothesis further. Guensburg and Sprinkle (2009) and Guensburg et al. (2016) regard edrioasteroid echinoderms, such as the stromatocystidid *Cambraster* or the edrioblastoid *Cambroblastus*, to possess apomorphies indicating they share a more recent common ancestor with crinoids than with other echinoderms. Although this hypothesis contrasts with previous studies regarding edrioasteroids as stem group eleutherozoans (Paul and Smith, 1984; Smith 1984, 1985, 1990; Smith and Zamora, 2013), recent investigations suggest that edrioasteroids may comprise a para- or polyphyletic group (Kammer et al., 2013; Zamora 2013; Zamora and Rahman, 2014). Some edrioasteroids, such as the isorophids, may be closely related to gogiid eocrinoids, whereas other edrioasteroids, such as *Cambraster*, may be closer to glyptocystitoid blastozoans and crinoids (Kammer et al., 2013; Zamora et al., 2013; Zamora and Rahman, 2014). Because a comprehensive, up-to-date phylogeny of pentaradiate echinoderm lineages is currently lacking, we tentatively follow Guensburg and Sprinkle (2009) and Guensburg et al. (2016) by
including both *Cambraster* and the edrioblastoid *Cambroblastus* as additional external taxon specifiers.

Identifying synapomorphies of the Clade Crinoidea requires a phylogenetic hypothesis of their position within the broader echinoderm clade. As discussed above, this remains an open question. Basal members of both the Camerata and Pentacrinoidea have a dicyclic calyx with an irregular field of plates intercalating between fixed proximal brachials, suggesting these may be plesiomorphic traits (cf. *Apektocrinus*, *Cnemecrinus*, *Glenocrinus*) (Guensburg 2012, Ausich et al., 2015; Cole, in press; Wright, in press), but a definitive list of shared derived traits cannot be provided here. Moreover, it is challenging to propose a list of apomorphies that unambiguously differentiate crinoids from other echinoderm taxa because many traits are not exclusive to crinoids. Crinoids have been traditionally recognized as distinct from blastozoan-grade echinoderms in having true “arms”, where arms are defined as coelomic extensions of the body cavity (Sprinkle, 1973). However, morphologic observations of solute and diploporitan echinoderms such as *Eumorphocystis*, as well as the discovery of various Cambrian ‘blastozoans’ with arm-like appendages strongly suggest that arms may not be an apomorphy unique to crinoids (Clausen et al., 2009; Zamora and Smith, 2011; Sumrall, 2014; Zamora and Rahman, 2014).

We anticipate future phylogenetic research will help resolve these broader issues in echinoderm phylogeny and evolution. Improved knowledge of relationships among extinct pentaradiate echinoderms may also help refine our definition of the Clade Crinoidea by removing pleonastic external specifiers. We await its refinement.
Definition.—The Camerata is stem-defined as the most inclusive clade containing *Actinocrinites triacontadactylus* Miller, 1821 and *Rhodocrinites verus* Miller, 1821 but not *Pentacrinites fossilis* Blumenbach, 1804.

Remarks.—Camerate crinoids represent a diverse, morphologically distinct “stem clade” *(sensu* Sereno, 1999; 2005) ranging from the Lower Ordovician to Permian and contain all taxa traditionally placed within the Diplobathrida and Monobathrida (Moore and Teichert, 1978; Cole, in press). Camerates are most easily differentiated from pentacrinoids in having calyx plates united by rigid sutures, a heavily plated tegmen surface covering the mouth, and a medial plate (or series of plates) in the posterior (i.e., CD) interray. Unlike pentacrinoids, the camerate posterior plate series has no proximal topographic affinity with the C ray, although some camerate posterior plates may be homologous with those of pentacrinoids (see Jaekel, 1918, p. 46; Moore and Laudon, 1943; Brower, 1973, p. 301–304; Guensburg and Sprinkle, 2003). In addition, typical camerate species have fixed proximal brachials, interradials, and sometimes intrabrachials, whereas most derived pentacrinoid clades lack these features.

Multiple studies indicate strong support for camerate monophyly (Ausich, 1998b; Ausich et al., 2015; Cole, in press). However, Cole’s (in press) analysis of Ordovician camerates did not find support for a strict division between monocyclic and dicyclic forms. Cole’s (in press) phylogenetic revision proposed narrower restrictions on clade
membership to render these taxa monophyletic. Following revision, the Monobathrida and Diplobathrida are sister clades that together comprise the more inclusive Eucamerata (Cole, in press). Thus, the stem-based definition of the Camerata contains the Clade Eucamerata and their stem taxa, including representatives of the oldest known crinoid fossils (e.g., *Eknomocrinus*, *Cnemecrinus*), genera placed within the problematic Reteocrinidae (see Cole, in press), and may or may not contain the protocrinoids (see Guensburg and Sprinkle, 2003; Guensburg, 2012; Ausich et al., 2015; Cole, in press).

**Eucamerata Cole, in press**

*Definition.*— The Eucamerata is node-defined as the least inclusive clade containing *Actinocrinites triacontadactylus* Miller, 1821, *Rhodocrinites verus* Miller, 1821, and *Rosfacrinus robustus* LeMenn and Spjeldnaes, 1996.

*Remarks.*— Cole (in press) revised the Monobathrida and Diplobathrida to represent monophyletic groups while attempting to preserve the greatest number of taxa traditionally included within each (Moore and Teichert, 1978). The name Eucamerata was proposed to identify the clade of camerate taxa comprised of the sister groups Monobathrida and Diplobathrida, which necessarily excludes stem taxa such as *Cnemecrinus* and *Reteocrinus* (Cole, in press). The Eucamerata comprise the vast majority of camerate taxa and span the Ordovician through Permian. Eucamerates are characterized generally by the traits listed above for the Camerata, but differ in typically
having more strongly ankylosed calyx plate sutures, primaxils on the second primibrachial, holomeric stems, and pinnulate arms (cf. *Actinocrinites* and *Rhodocrinites* with *Eknomocrinus* and *Reteocrinus*).

In an attempt to preserve the stability of sister group relationships between monobathrid and diplobathrid clades, we provide a node-based definition for the Eucamerata and stem-based definitions for the Monobathrida and Diplobathrida. The internal taxon specifiers *Actinocrinites* and *Rhodocrinites* are highly-nested constituents of their respective monobathrid and diplobathrid subclades (Moore and Laudon, 1943; Cole, in press). *Rosfacrinus* is cautiously included as an additional external specifier because it occupies a somewhat uncertain position at the base of the eucamerate tree (see discussion in Cole, in press).

**Monobathrida Moore and Laudon, 1943**

*Definition.*— The Monobathrida is stem-defined as the most inclusive clade containing *Glyptocrinus decadactylus* Hall, 1847 and *Actinocrinites triacontadactylus* Miller, 1821 but not *Rhodocrinites verus* Miller, 1821 and *Archaeocrinus lacunosus* (Billings, 1857).

*Remarks.*—When revising Bather’s (1899) polyphyletic division of crinoids into the Monocyclica and Dicyclica, Moore and Laudon (1943) placed all camerates with monocyclic calyces into the Monobathrida. Cole’s (in press) phylogenetic analysis of Ordovician camerate crinoids indicates a strict adherence to Moore and Laudon’s (1943)
concept of the Monobathrida is not monophyletic. However, removal of the basal camerates *Eknomocrinus* and *Adelphicrinus* renders the Monobathrida a clade (Cole, in press). The internal and external specifiers defining this stem-based clade ensure the taxonomic content closely matches Moore and Laudon (1943).

Monobathrids are a taxonomically diverse group of camerates ranging from the Ordovician to Permian and are traditionally diagnosed as monocyclic camerates. Although other clades had similar trends in circlet reduction (e.g., the Disparida), the transformation from a dicyclic to monocyclic calyx likely represents a veritable synapomorphy of monobathrid camerates, as the dicyclic crinoid *Gaurocrinus* was recovered as the sister taxon to the Monobathrida by Cole (in press). Additional features diagnostic of a typical monobathrid species include having radial plates larger than other calyx plates, an upright basal circlet, an uninterrupted radial circlet (except in the posterior interray), and a posterior interray with anitaxis plating and an anitaxial ridge.

**Diplobathrida** Moore and Laudon, 1943

*Definition.*—The Diplobathrida is stem-defined as the most inclusive clade containing *Archaeocrinus lacunosus* (Billings, 1857) and *Rhodocrinites verus* Miller, 1821 but not *Actinocrinites triacontadactylus* Miller, 1821 and *Glyptocrinus decadactylus* Hall, 1847.

*Remarks.*—Similar to the discussion above, Moore and Laudon (1943) placed all of Bather’s (1899) dicyclic camerate crinoids within the Diplobathrida. As with the
monobathrids, Cole’s (in press) phylogenetic analysis of Ordovician camerates revealed Moore and Laudon’s (1943) Diplobathrida required revision. To achieve monophyly of diplobathrids while retaining much of Moore and Laudon’s (1943) taxonomic content, all dicyclic stem taxa equally related to both monobathrid and diplobathrid camerates *sensu* Cole (in press) are removed from the Diplobathrida (e.g., *Eknomocrinus*, *Reteocrinids*, etc.). Following Cole’s (in press) suggested revision, our stem-based definition stabilizes the long-held hypothesis that monobathrids and diplobathrids represent sister clades (Moore and Laudon, 1943; Cole, in press).

Diplobathrids range from the Ordovician through lower Carboniferous (Serpukhovian). Cole’s (in press) discussion on the taxonomic distribution of diplobathrid morphologies suggests they are generally characterized by a combination of character states, including a dicyclic calyx, a concave calyx base either concealing or partially concealing the infrabasal plates, and the presence of additional plates interrupting the radial circlet in all interrays (e.g., *Rhodocrinites*). Some diplobathrids *sensu* Cole (in press), such as the Dimerocrinitidae, are similar to monobathrids in having their radial circlet interrupted only in the posterior interray but can easily be distinguished by their dicyclic calyx. A closer examination of post-Ordovician species indicates a substantial revision of subclades within the Diplobathrida is needed and additional research is currently underway (Cole, 2015)
Definition.—The Pentacrinoidea is stem-defined and as the most inclusive clade containing *Apektocrinus ubaghsi* Guensburg and Sprinkle, 2009 and *Pentacrinites fossilis* Blumenbach, 1804 but not *Rhodocrinites verus* Miller, 1821 and *Actinocrinites triacontadactylus* Miller, 1821.

Remarks.—The name Pentacrinoidea originates from Jaekel’s (1894; 1918) prescient observation that camerate and non-camerate crinoid form distinct clades. Although authors after Jaekel (1918) did not adopt this name in subsequent classifications (see Lane, 1978; Ausich and Kammer, 2001), Jaekel’s usage coincides with this strongly supported clade (Guensburg, 2012; Ausich et al., 2015; Cole, in press; Wright, in press). Thus, we propose to reinstate the name Pentacrinoidea with the definition above.

We have chosen two phylogenetically distant non-camerate species as internal specifiers. *Pentacrinites fossilis* is a well-known fossil species from rocks of Jurassic age and is closely related to extant isocrinid crinoids (David et al., 2006), placing it within the Crown Crinoidea (see Articulata below). The species *Apektocrinus ubaghsi* is a Lower Ordovician fossil and ranks among the stratigraphically oldest known crinoids (Guensburg and Sprinkle, 2009). However, all phylogenetic research indicates it is closer to non-camerates than camerates and diverges stemward of other basal ‘cladid’ (*sensu* Moore and Teichert, 1978) taxa such as *Aethocrinus* (Guensburg and Sprinkle, 2009; Guensburg 2012; Ausich et al., 2015; Wright, in press). Our stem-based definition
recognizes Jaekel’s (1918) priority of this concept and effectively places all known non-camerate species within the Pentacrinoidea.

Pentacrinoids are a spectacularly diverse and morphologically heterogeneous clade ranging from the Early Ordovician to present day marine communities. The primary apomorphies differentiating pentacrinoids from camerates relate to their distinctive posterior plating patterns, the degree of calyx plate suturing, and oral region rigidity (‘tegmen’ terminology here is from Ausich and Kammer, 2016). Posterior plates among pentacrinoids display a proximal relationship with the C-ray radial plate (Guensburg 2010; Wright, 2015a). Subclades within the Pentacrinoidea express this affinity differently (cf. Cladida and Disparida), and extant crinoids do not retain posterior plates as adults. However, the ontogenetic trajectory of posterior plate development in extant crinoids is tightly linked with morphologic patterns among their Paleozoic precursors (Wright, 2015a). Pentacrinoid calyx plates are less closely sutured (i.e., ankylosed) than camerates and typically have a non-rigid to flexible oral region. In many pentacrinoids, the mouth is directly exposed on the oral surface rather than beneath a tegmen (Ausich and Kammer, 2016).

There are several other morphologic features less diagnostic than those described above but still useful for distinguishing most pentacrinoid species from camerates. For example, some basal pentacrinoids such as *Apektocrinus, Aethocrinus,* and *Alphacrinus* incorporate additional plates within the calyx (similar to camerates). However, the overwhelming majority of pentacrinoid clades do not. A major exception occurs among flexible crinoids, but flexibles are a derived group of pentacrinoids and can be
differentiated from camerates by other apomorphies (see Flexibilia below). Similarly, eucamerate crinoids have pinnules but most early to middle Paleozoic pentacrinoids do not. Pinnulation evolved at least once (and probably several times) during the middle to late Paleozoic among the subclade Cladida (Wright, 2015b), but these taxa can readily be distinguished from eucamerates in having a pentacrinoid-like posterior plating pattern and free arms above the radials.

Inadunata Wachsmuth and Springer, 1885

Definition.—The Inadunata is node-defined and is the least inclusive clade containing *Synbathocrinus conicus* Phillips, 1836 and *Dendrocrinus longidactylus* Hall, 1852.

Remarks.—Wachsmuth and Springer (1885) placed non-articulate fossil crinoids with free arms above the radial plates within the Inadunata. Subsequent classifications divided the Inadunata into the Cladida and Disparida based on the number of circlets in the calyx (Moore and Laudon, 1943; Moore and Teichert, 1978). In a pioneering study on phylogenetic approaches to crinoid classification, Simms and Sevastopulo (1993) pointed out the Inadunata of Moore and Teichert (1978) was paraphyletic and recommended the name be abandoned. In addition, Simms and Sevastopulo’s (1993) revision resolved the paraphyly of cladid inadunates by including the Flexibilia and Articulata within the Cladida.
The division between the Camerata and Pentacrinoida (discussed above) indicates disparids and cladids are more closely related to one another than to camerates (Fig 4.2). Indeed, recent phylogenetic analyses of Ordovician crinoids recover a sister group relationship between disparids and cladids (sensu Moore and Laudon, 1943), with hybocrinids nested within the Cladida (Fig. 4.2) (Guensburg, 2012; Ausich et al., 2015; Wright, in press). Our definition of the Inadunata combines Wachsmuth and Springer’s (1885) original concept with Simms and Sevastopulo’s (1993) revision of the Cladida to include flexibles and articulates. Note that this definition places basal pentacrinoids, such as *Apektocrinus*, outside the Inadunata. We combine a node-based definition of the Inadunata with stem-based definitions for the subclades Disparida and Cladida to form a node-stem triplet to increase the stability of sister relationships between these taxa (Sereno, 1999).

The Clade Inadunata ranges from the Early Ordovician to the present and are as a whole well-characterized by Wachsmuth and Springer’s (1885) general concept of crinoids with free arms above the radial plates. Exceptions to this diagnosis occur but are mostly restricted to a few possibly basal taxa and the Flexibilia, which represent a derived group of inadunates (Springer, 1920).

Disparida Moore and Laudon, 1943

Definition.—The Disparida is stem-defined as the most inclusive clade containing *Synbathocrinus conicus* Phillips, 1836 but not *Dendrocrinus longidactylus* Hall, 1852.
Remarks.—Disparids comprise a diminutive but morphologically and taxonomically diverse clade of fossil crinoids ranging from the Ordovician through Permian. Moore and Laudon (1943) erected the Disparida to include all monocyclic inadunates. Disparid monophyly is well-supported by phylogenetic analyses of Ordovician crinoids (Guensburg, 2012; Ausich et al., 2015; Wright, in press) and contains all species closer to *Synbathocrinus* than the cladid *Dendrocrinus*. Given the similar topologies across these studies, the Clade Disparida retains taxa traditionally placed within disparids (*sensu* Moore and Laudon, 1943) except for the hybocrinids.

A major synapomorphy and useful diagnostic trait of disparid crinoids is the presence of a single circlet of plates below the radials. All other pentacrinoids are either dicyclic (cladids), pseudomonocyclic (hybocrinids) (see Sprinkle, 1982a), or otherwise phylogenetically distant from disparids (some derived articulates may not develop infrabasals, see Lahaye and Jangoux, 1987). Disparids also have simple or compound radial plates, typically lack pinnules, and approximate bilateral symmetry between rays oriented in one of several possible planes (see Moore et al, 1978). As pentacrinoids, disparids have posterior plates in a proximal position to the C ray but differ from cladids in having plates positioned above rather than below or in-line with the C-ray radial plate. However, posterior plate homologies among disparids and between inadunate clades are presently obscured by a set of descriptive terms opaque to homology. Whether the proximal C-ray posterior plate is an “anibrachial”, “radianal”, “anal X”, “superradial”, or a “radial” is uncertain (Moore, 1962; Moore and Teichert, 1978; Ausich, 1996). Future
work is needed to help clarify primary posterior plate homologies among disparids and between cladids and disparids. The results of Wright’s (in press) analysis of Ordovician through Devonian pentacrinoid taxa support Guensburg’s (2010) assessment of *Alphacrinus* as a lower Tremadocian crinoid phylogenetically close to the base of the disparid clade. Guensburg (2010) considered the posterior of *Alphacrinus* to express a transitional form between “typical” pentacrinoid posterior plates and the ray-like extensions common among disparid taxa. A re-examination of the posterior interray of basal taxa combined with studies on disparid ontogeny may help resolve this issue.

Cladida Moore and Laudon, 1943

*Definition.*—The Cladida is stem-defined as the most inclusive clade containing *Dendrocrinus longidactylus* Hall, 1852 but not *Synbathocrinus conicus* Phillips, 1836.

*Remarks.*—The Cladida were originally defined by Moore and Laudon (1943) to comprise a tremendously diverse and long-ranging (Ordovician–Triassic) assemblage of dicyclic inadunates with their mouths covered with primary peristomial cover plates (Ausich and Kammer, 2016). Moore and Laudon’s (1943) original concept and taxonomic content of the Cladida is paraphyletic, as they agreed with Springer’s (1920) earlier assessment that flexible crinoids were more closely related to some cladids than others but did not place the Flexibilia within the Cladida. Moreover, post-Paleozoic crinoids within Miller’s (1821) Articulata have long been considered descendants of
Paleozoic cladids (Jaekel, 1918; Moore et al., 1952; Rasmussen, 1978; Simms, 1988). Simms and Sevastopulo (1993) conducted a cladistic analysis of Paleozoic cladids, flexibles, and articulate crinoids and subsequently remedied cladid paraphyly by placing the Flexibilia and the Articulata within the Cladida (*sensu* Moore and Laudon, 1943). Although many authors have followed Simms and Sevastopulo’s (1993) interpretations of relationships among these taxa, only a few authors have since followed their revised rank-based classification (e.g., Brower, 2001, 2002; Donovan and Harper, 2003).

Our stem-based definition of the Cladida is similar in taxonomic content to Simms and Sevastopulo (1993) because it includes all species closer to *Dendrocrinus* than to the disparid *Synbathocrinus*. Thus, the Cladida spans the Ordovician to the Recent and contains the major subclades Porocrinoidea, Flexibilia, and Articulata. Cladids are most easily distinguished from their sister group, the Disparida, in typically having a dicyclic calyx and posterior plates (as adults or during development) located below and/or in-line with the radial plate circle (Wright, 2015a). Lastly, many middle Paleozoic to Recent cladids have pinnules, whereas most disparids do not (Frest et al., 1979).

**Porocrinoidea Wright, in press**

*Definition.*—The Porocrinoidea is node-defined and is the least inclusive clade containing *Carabocrinus radiatus* Billings, 1857 and *Hybocrinus conicus* Billings, 1857.
Remarks.—In their description of crinoids belonging to Bather’s (1899) ‘Cyathocrinina’, Moore and Laudon (1943) speculated that “primitive” cyathocrinoids such as *Carabocrinus* might be closely related to the enigmatic taxon *Hybocrinus*. Sprinkle (1982a) argued the stem and calyx morphology of *Hybocrinus* suggested hybocrinids were “pseudomonocyclic” and listed a number of characters linking hybocrinids with cladids. Although hybocrinids have not traditionally been classified within the Cladida, many phylogenetic analyses of Ordovician crinoids have recovered a clade of ‘cyathocrine’ grade cladids and hybocrinids (Guensburg, 2012; Ausich et al., 2015; Wright, in press). Wright’s (in press) phylogenetic analysis of Ordovician through Devonian pentacrinoids recovered a clade comprised of *Porocrinus, Carabocrinus*, and the hybocrinids *Hybocrinus* and *Hybocystites*. Notably, this clade is stemward of the split between flexible and other cladid crinoids. Thus, Wright (in press) proposed the name Porocrinoidea to encompass this early diverging and morphologically unique clade of Ordovician crinoids.

Our node-based definition of the Porocrinoidea sets up a node-stem triplet that stabilizes the sister clade relationship among the Porocrinida and Hybocrinida recovered by Ausich et al. (2015), which had denser taxon sampling of Ordovician crinoids than Wright (in press). The Clade Porocrinoidea is likely limited to the Ordovician Period, but additional analyses sampling younger species are needed to test the extent of their geologic duration. Porocrinoids are a subclade of cladids characterized by globose, conical, or ovate calyces that possess a number of apomorphies convergent with blastozoan echinoderms, such as having thecal respiratory structures, reduction in arm
number and calyx plates, and/or recumbent ambulacra (see Moore and Teichert, 1978; Sprinkle, 1982a, 1982b).

Porocrinida Miller and Gurley, 1894

**Definition.**—The Porocrinida is stem-defined as the most inclusive clade containing *Porocrinus conicus* Billings, 1857 and *Carabocrinus radiatus* Billings, 1857 but not *Hybocrinus conicus* Billings, 1857.

**Remarks.**—The Porocrinida comprise a small clade of Ordovician porocrinoids with apomorphic endothecal and/or exothecal respiratory structures. Sprinkle (1982b) pointed to many similarities among *Carabocrinus*, *Palaeocrinus*, and the Porocrinidae and hypothesized they may be closely related. Ausich et al. (2015) recovered a topology supporting this hypothesis with the Euspirocrinid *Illemocrinus* as their sister taxon. However, Wright (in press) recovered *Euspirocrinus* outside the porocrinid clade within a different clade of ‘cyathocrine’ grade cladids. Thus, *Illemocrinus* is tentatively placed within the Porocrinida, but other taxa within the Euspriocrinidae should not be placed within the Porocrinida at this time as additional revisions are necessary. Guensburg (2012) recovered a similar tree to Ausich et al. (2015) that suggested *Perittocrinus* may be also be a porocrinid.

The stem-based definition of the Porocrinida makes them sister to the Hybocrinida and retains the taxonomic membership of this clade recovered in Ausich et
Porocrinids can easily be distinguished from hybocrinids in having a dicyclic calyx and the presence of thecal respiratory structures (Kesling and Paul, 1968; Sprinkle, 1982b).

Hybocrinida Jaekel, 1918

**Definition.**—The Hybocrinida is stem-defined as the most inclusive clade containing *Hybocrinus conicus* Billings, 1857 and *Hybocystites problematicus* Wetherby, 1880 but not *Porocrinus conicus* Billings, 1857 and *Carabocrinus radiatus* Billings, 1857.

**Remarks.**—Hybocrinids comprise a small yet morphologically disparate clade of Ordovician crinoids. Although the monocyclic hybocrinids have either been considered disparids or classified outside the Inadunata (Moore and Laudon, 1943; Moore and Teichert, 1978; Ausich 1998b), Sprinkle (1982a) suspected hybocrinids might be “pseudomonocyclic” and potentially related to ‘cyathocrine’ cladids (see Sprinkle, 1982a, 1982b). Phylogenetic analyses by Guensburg (2012), Ausich et al. (2015), and Wright (in press) all support the monophyly of the Hybocrinida and their sister group relationship with taxa placed in the Porocrinida (see Sprinkle, 1982a).

In addition to having a “pseudomonocyclic” calyx (infrabasals absent), hybocrinids are characterized by a number of unusual apomorphies that distinguish them from Porocrinids (and all other crinoids). Many of these traits are similar to those typically present in blastozoan echinoderms, including reduction in the number of arms,
modification of food-gathering appendages to be recumbent (sometimes extending downward over calyx plates), and reduction in the number of calyx plates (Sprinkle and Moore, 1978).

Flexibilis Zittel, 1895

*Definition.*—The Flexibilis is stem-defined as the most inclusive clade containing *Taxocrinus macrodactylus* (Phillips, 1841) but not *Dendrocrinus longidactylus* Hall, 1852.

*Remarks.*—Flexible crinoids are a morphologically homogeneous clade that originated sometime during the Middle to Late Ordovician and range through the Permian. Frank Springer (1911, 1920) was the first to recognize that flexible crinoids were closely related to inadunates. In his comprehensive 1920 monograph, *The Crinoidea Flexibilis*, Springer compared morphologic characteristics of the inadunate *Cupulocrinus* with the earliest known flexible *Protaxocrinus*, citing numerous similarities in calyx plating, interradial areas, and the arrangement of posterior plates. Springer (1920) concluded *Cupulocrinus* was potentially a transitional fossil that linked inadunates with flexibles, stating, “there is clearly an intermingling of the characters… and it is evident that in *Cupulocrinus* we have to deal with a transition [sic] form whose exact status is difficult to decide” (Springer, 1920, p. 89). Subsequent taxonomic treatments have also recognized *Cupulocrinus* as
occupying a proximal position to the base of the flexible tree (Moore and Laudon, 1943; Moore and Teichert, 1978).

Phylogenetic analyses sampling flexible and other crinoid taxa have invariably recovered tree topologies supporting Springer’s (1911, 1920) hypothesis, with *Cupulocrinus* recovered as the sister taxon to Flexibilia (Brower, 1995, 2001; Ausich, 1998b; Ausich et al., 2015; Wright, in press). Wright’s (in press) analysis used Bayesian methods to estimate the probability of *Cupulocrinus* being ancestral (*sensu* Foote, 1996) to the flexible clade. Results strongly support *Cupulocrinus* as occupying an ancestral position (posterior probability = 0.99) (Wright, in press). Given these results and our stem-based definition of the Flexibilia, species of *Cupulocrinus* are now placed within the flexibles.

Flexible crinoids have loosely-sutured calyx plating and a remarkably uniform set of apomorphies relative to other crinoid clades. For example, flexibles differ from cladids in having interradial and intrabrachial plates and differ from other dicyclic crinoids in typically having their lowermost circllet comprised of three (rather than five) infrabasal plates. One infrabasal plate, the “azygous”, is smaller than the other two that formed by fusion and is located in the C ray (except for the derived *Forbesiocrinus*). Many flexibles retain posterior plate arrangements similar to other cladids, but posterior plates are sometimes absent in more derived flexibles. In contrast with cladids, arms of flexible crinoids are universally uniserial and lack pinnules, and the stem is nearly always transversely circular (Springer, 1920).
Eucladida Wright, in press

**Definition.**—The Eucladida is stem-defined as the most inclusive clade containing *Dendrocrinus longidactylus* Hall, 1952 and *Pentacrinites fossilis* Blumenbach, 1804 but not *Taxocrinus macrodactylus* (Phillips, 1841).

**Remarks.**—The revision of the Cladida to be monophyletic requires placing the subclades Porocrinoidea, Flexibilia, and Articulata within a more inclusively defined Clade Cladida (Simms and Sevastopulo, 1993; Wright, in press). However, the Cladida (*sensu* Moore and Laudon, 1943) is traditionally conceived as a Paleozoic-age paraphyletic group that excludes the Flexibilia. The Eucladida was proposed by Wright (in press) to comprise all species within the Clade Cladida sharing a more recent common ancestor with *Dendrocrinus* and *Pentacrinites* than with *Taxocrinus*. Thus, the stem-based clades Flexibilia and Eucladida are sister to one another and articulates are nested within the Eucladida. This Eucladida retains much of the meaning and taxonomic content of Moore and Laudon’s (1943) concept for Paleozoic cladids while eschewing paraphyly.

In the *Treatise on Invertebrate Paleontology*, Moore et al. (1978) recognized three rank-based taxa within the Cladida: the Dendrocrinida, the Cyathocrinida, and the Poteriocrinida. However, it has long been questioned whether or not these taxa represent monophyletic groups (McIntosh, 1986; 2001; Sevastopulo and Lane, 1988; Simms and Sevastopulo, 1993; Kammer and Ausich, 1992, 1996; Wright, 2015a, 2015b; Wright and Ausich, 2015). Indeed, the Poteriocrinida is depicted in the *Treatise* as a polyphyletic
group (Moore et al., 1978, fig. 412). A phylogenetic analysis of Ordovician through Devonian pentacrinoïds by Wright (in press) has confirmed the doubts over the monophyly of these taxa. Much of the problem arises from ambiguous and/or uninformative apomorphies chosen for these taxa that perpetuate taxonomic anarchy via “undiagnostic diagnoses” (Wright, 2015b, see Lane, 1978, p. T295). Although much revision is needed, recent analyses indicate there is nevertheless considerable phylogenetic structure among subclades of Paleozoic cladids and additional work is underway to revise this diverse group (Wright, 2015b).

Articulata Miller, 1821

**Definition.**—The Articulata is node-defined as the least inclusive clade containing *Endoxocrinus parrae* (Gervais, 1835) and *Antedon bifida* (Pennant, 1777).

**Remarks.**—The Articulata was proposed by Miller (1821) and has since developed a longstanding reputation as a problematic group that lacks a concise and unambiguous definition (Rasmussen, 1978; Simms, 1988; Simms and Sevastopulo, 1993; Webster and Jell, 1999; Rouse et al., 2013). Although all extant crinoids are invariably recognized as articulates, much confusion surrounds the recognition of fossil articulates and the timing of their origin. The primary difficulties surround which apomorphy (or combination of apomorphies) is useful for diagnosing the Articulata. For example, it is widely appreciated that no apomorphy or unique set of apomorphies can presently diagnose
fossil articulates without ambiguity (Simms, 1988; Simms and Sevastopulo, 1993; Webster and Jell, 1999; Rouse et al, 2013). Most crinoid workers have obviated this problem by simply treating the Articulata as synonymous with post-Paleozoic crinoids (see Simms and Sevastopulo, 1993). However, this usage is problematic because this definition is not based on any explicit phylogenetic hypothesis. Moreover, many Paleozoic groups of fossil cladids share different combinations of traits typically listed as “diagnostic” for the Articulata (Webster and Jell, 1999; Webster and Lane, 2007). If the concept of what defines the Articulata depends on the choice of a particular combination of apomorphies alone, then questions regarding the “origin of the Articulata” will always depend on which specific combination was chosen \textit{a priori} to be diagnostic. Without a phylogenetic definition, it is impossible to objectively specify a precise set of synapomorphies for the Articulata. Thus, we propose herein to define the Articulata as the crinoid crown group containing the last common ancestor of the extant isocrinid \textit{Endoxocrinus parrae} and the comatulid \textit{Antedon bifida}, and all of its descendants.

As discussed by Ruta et al. (2003), the concepts of stem groups and crown groups are sometimes misinterpreted or misused in the paleontological literature. Used properly, crown groups are defined by extant taxon specifiers. Notably, crown groups may be comprised of many (or mostly) extinct fossil species. For example, if a fossil crinoid is more closely related to some extant species than others, it is a member of the crown group. According to Rouse et al. (2013), the most recent common ancestor of all extant crinoids lived sometime during the Middle to Upper Triassic. Thus, our node-based definition eliminates the non-phylogenetic concept of “post-Paleozoic Crinoidea” while
retaining the majority of post-Paleozoic crinoids traditionally included within the Articulata. The Clade Articulata is synonymous with the Crown Crinoidea (Sumrall, 2014), and we advocate workers use these terms interchangeably depending on context (e.g., discussing relationships among crinoids or between crinoids and non-crinoids). Traits that may be present in the Articulate ancestor are listed in Simms (1988), Simms and Sevastopulo (1993), Webster and Jell (1999), and Rouse et al. (2013).

The Articulata likely contains most post-Paleozoic taxa traditionally considered articulates, including the ~600 or so extant species. Although our definition of the Articulata is defined with precision and phylogenetic stability (Rouse et al., 2013; Rouse et al., 2015), it remains difficult in practice to unambiguously identify fossil articulates, particularly among specimens near the base of the articulate tree. However, such difficulties are already present and have long obfuscated the origin of the crinoid crown group. The more important problem is resolving the phylogenetic position of the common ancestor of extant crinoids within the myriad of fossil lineages. Our definition provides a useful framework for future phylogenetic research to uncover relationships between potential stem articulates, extinct crown group lineages, and extant species.

**A revised rank-based classification of the Crinoidea**

Crinoid clades identified herein confirm many long-held views on the major divisions among crinoids from both the foundational work of Moore and Laudon (1943) and
Moore and Teichert (1978) to more recent analyses (i.e., Ausich, 1998a, 1998b; Guensburg and Sprinkle, 2003; Guensburg, 2012; Ausich et al., 2015). Results from all of these studies recognized the Camerata, Diplobathrida, Monobathrida, Hybocrinida, Disparida, Cladida, and Flexibilia. The challenge is to represent these widely recognized clades in a rank-based Linnaean classification scheme that maximizes common usages of names for crinoid lineages (Moore and Teichert, 1978) and is consistent with a phylogenetic understanding of relationships (Wiley and Lieberman, 2011). In our revision, the Crinoidea remain a class and every attempt is made to retain orders as recognized in Moore and Teichert (1978). Unfortunately, the tree topology of Figure 4.2 prevented the attainment of the latter in all instances, but the addition of intermediate Linnaean ranks makes it easier to apply a phylogenetic perspective to rank-based crinoid classification. The use of intermediate ranks (e.g., Parvclass) follows traditional use in pre-existing taxonomic literature (see Carroll 1988; Sibley, 1994; Benton, 2005). Two older taxonomic names, the Pentacrinoidea Jaekel, 1918 and Inadunata Wachsmuth and Springer, 1885, are formally reinstated herein because they represent meaningful clades as described above.

Post-Ordovician cladids (*sensu* Moore and Laudon, 1943) and the Protocrinoida (Guensburg and Sprinkle, 2003) remain problematic groups. Because the rank for a monophyletic Cladida must be above flexibles and articulates (Simms and Sevastopulo, 1993), we propose the name Cyathoformes to contain taxa traditionally placed within the Cladida that are sister to the Articulata. Relationships among these taxa are the subject of future phylogenetic research (Wright, 2015b) and are not treated further here. From their
initial description (Guensburg and Sprinkle, 2003), the protocrinoids have been an important but confounding group of crinoids that display characteristics of both crinoids and other stalked echinoderms. Guensburg and Sprinkle (2003) regarded the protocrinoid as an “order (plesion)”’. The validity of the protocrinoids was later questioned by Guensburg and Sprinkle (2009) and led Guensburg (2012) to formally place them within the Camerata. However, Ausich et al. (2015) recovered a sister group relationship between *Titanocrinus* and *Glenocrinus*, but with protocrinoids more closely related to non-camerates than camerates. In contrast, Cole’s (in press) analysis of Ordovician crinoids recovered the protocrinoids as more closely related to camerates than non-camerates. Thus, we have carefully chosen our clade definitions above to not depend on a particular phylogenetic hypothesis or morphologic interpretation of these significant but problematic taxa. For the moment, we tentatively place both protocrinoid taxa as Crinoidea *incertae sedis* subclass Protocrinoida.

In our present understanding of crinoid evolution, the first major divergence occurs between camerates and all other crinoids (Fig. 4.2). The subclass rank is retained for the Camerata; and the subclass Pentacrinoidea Jaekel, 1918 is proposed for its sister group (Table 3.2). Within the Camerata, the orders Diplobathrida and Monobathrida are retained as sister groups, and the infraclass Eucamerata Cole (in press) unites these two orders. In phylogenetic analyses of camerates, several taxa are not placed within the Monobathrida and Diplobathrida (*sensu* Cole, in press). Thus, they are considered here to be stem eucamerates (see remarks for Eucamerata above). The subclass Camerata unites these stem taxa with eucamerates.
In terms of species richness, the subclass Pentacrinoidea is the largest crinoid clade. This includes the Disparida, Cladida, Hybocrinida, and Articulata of Moore and Teichert (1978), which coincides exactly with the Jaekel’s (1918) concept of the Pentacrinoidea (see Lane, 1978). Hence, we have proposed the reinstatement of this name. The Pentacrinoidea is comprised of the infraclass Inadunata and their stem taxa (e.g., *Apektocrinus*). The concept for the Inadunata in Moore and Teichert (1978) united the Disparida and the Cladida. Here, the infraclass Inadunata unites the Disparida, Cladida, and all of their descendants, the latter of which were traditionally placed outside the Cladida. This usage circumvents the non-phylogenetic usage of the Inadunata (*sensu* Moore and Teichert, 1978) and is consistent with the phylogenetic conclusions of Simms and Sevastopulo (1993). With the Inadunata an infraclass, the Disparida and Cladida are both parvclasses. Taxa placed within the Disparida are in need of revision and current work is underway to establish relationships among subclades (Ausich and Donovan, 2015).

Within the Cladida, the Hybocrinida, Porocrinida, Taxocrinida Springer, 1913; and Sagenocrinida Springer, 1913 are orders (Table 2). The orders Hybocrinida and Porocrinida are sister groups forming the superorder Porocrinoida Wright (in press). The Flexibilia are transferred to the superorder rank which is comprised of the two sister groups, order Taxocrinida and order Sagenocrinida. The Cyathoformes and Articulata comprise the magnorder Eucladida (Wright, in press). The Eucladida retains most cyathocrinids, dendrocrinids, and poteriocrinids of Moore and Teichert (1978). As discussed above, phylogenetic relationships within this clade await further study (Wright,
Analyses detailing the late Paleozoic and early Mesozoic crinoid phylogeny are needed to understand this crucial period of crinoid evolution. Lastly, the Articulata is considered a superorder within the Cladida.

Conclusions

A phylogeny-based revision of crinoid systematics is proposed to clarify the definition of clades and inform a major revision of the rank-based Linnaean classification. These revisions are based on recent computational phylogenetic analyses that build on the historic subdivision of crinoids into major lineages. It is hoped that the phylogenetic classification schemes presented herein will help provide a framework for future research on crinoid phylogeny and offer guidance to crinoid workers and non-specialists alike interested in using this fascinating group of echinoderms to study evolutionary patterns and processes.
References


Ausich, W.I., 1998b, Phylogeny of Arenig to Caradoc Crinoids (Phylum Echinodermata) and suprageneric classification of the Crinoidea: The University of Kansas Paleontological Contributions Papers, New Series, no. 9, 36 p.


Carlson, S.J., and Leighton, L.R., 2001, The phylogeny and classification of


Clark, A. H. 1908. Description of new species of crinoids, chiefly from the collections
made by U.S. Fisheries steamer ‘‘Albatross’’ at the Hawaiian Islands in 1902,
with remarks on the classification of the Comatulida: Proceedings of the U.S.

Clark, A.H., 1915, A monograph of the existing crinoids, part 1: Bulletin of the United

Clark, A.H., 1921, A monograph of existing crinoids, part 2: Bulletin of the United States


Clausen, S., Jell, P.A., Legrain, X., and Smith, A.B., 2009, Pelmatozoan arms from the
Middle Cambrian of Australia: bridging the gap between brachioles and

Cohen, B.L., Ameziane, N., Eleaume, M., and de Forges, B.R., 2004, Crinoid phylogeny:
605–617.


Matsumoto, H., 1929, Outline of a classification of Echinodermata: Science Reports of the Tohoku Imperial University, Sendai, Japan, Second Series (Geology): v. 8, p. 27–33.


Paleobiology, v. 3, p. 74–82.

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., 1883, The American Palaeozoic fossils: a catalogue of the genera and
species, with names of authors, dates, places of publication, groups of books in
which found, and the etymology and significance of the words, and an
introduction devoted to the stratigraphical geology of the Palaeozoic rocks, 2nd

Miller, S.A. and Gurley, W.F.E., 1894, New genera and species of Echinodermata:

Le Cambrien et l’Arenig: Bulletin de la Société d’étude des Sciences naturelles de
Béziers v. 17, p. 5–36.

Mooi, R., and David, B., 1998, Evolution within a bizarre phylum; homologies of the

Mooi, R., and David, B., 2008, Radial symmetry, the anterior/posterior axis, and
echinoderm Hox genes: Annual Review of Ecology, Evolution, and Systematics,
v. 39, p. 43–62.


Moore, R.C., and Teichert, C., eds., 1978, Treatise on Invertebrate Paleontology, Part T, Echinodermata 2: Geological Society of America and University of Kansas Press, Lawrence, Kansas, 1027 p.


Phillips, J., 1841, Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon, and West Somerset; observed in the course of the ordinance geological survey of that district: London, Longmans, Brown, Green, and Longmans, 232 p.


Soul, L.C., and Friedman, M., 2015, Taxonomy and phylogeny can yield comparable results in comparative paleontological analyses: Systematic Biology, v. 64, p. 608–620.


Sumrall, C.D., 2008, The origin of Lovén’s Law in glyptocystitoid rhombiferans and its bearing on plate homology and heterochronic evolution of the hemicosmitoid


Table 4.1 Species name, least inclusive clade, and first appearances interval for each taxon depicted in Figure 4.1.
<table>
<thead>
<tr>
<th>Species</th>
<th>Least Inclusive Clade</th>
<th>First Occurrence of Species</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Actinocrinites triacontadactylus</em> Miller, 1821</td>
<td>Monobathrida</td>
<td>Mississippian (Tournaisian)</td>
</tr>
<tr>
<td><em>Adelphicrinus fortuitus</em> Guensburg and Sprinkle, 2003</td>
<td>Camerata</td>
<td>Ordovician (Tremadocian)</td>
</tr>
<tr>
<td><em>Alphacrinus mansfieldi</em> Guensburg, 2010</td>
<td>Disparida</td>
<td>Ordovician (Tremadocian)</td>
</tr>
<tr>
<td><em>Antedon bifida</em> (Pennant, 1777)</td>
<td>Articulata</td>
<td>Recent</td>
</tr>
<tr>
<td><em>Apektocrinus ubaghsi</em> Guensburg and Sprinkle, 2009</td>
<td>Pentacrinoidea</td>
<td>Ordovician (Tremadocian)</td>
</tr>
<tr>
<td><em>Archaeocrinus lacunosus</em> (Billings, 1857)</td>
<td>Diplobathrida</td>
<td>Ordovician (Katian)</td>
</tr>
<tr>
<td><em>Carabocrinus radiatus</em> Billings, 1857</td>
<td>Porocrinida</td>
<td>Ordovician (Sanbian)</td>
</tr>
<tr>
<td><em>Cupulocrinus heterocostalis</em> (Hall, 1847)</td>
<td>Flexibilia</td>
<td>Ordovician (Katian)</td>
</tr>
<tr>
<td><em>Dendrocrinus longidactylus</em> Hall, 1852</td>
<td>Eucladida</td>
<td>Silurian (Wenlockian)</td>
</tr>
<tr>
<td><em>Endoxocrinus parrae</em> (Gervais, 1835)</td>
<td>Articulata</td>
<td>Recent</td>
</tr>
<tr>
<td><em>Eknomocrinus wahlwahensis</em> Guensburg and Sprinkle, 2003</td>
<td>Camerata</td>
<td>Ordovician (Tremadocian)</td>
</tr>
<tr>
<td><em>Glyptocrinus decadactylus</em> Hall, 1847</td>
<td>Monobathrida</td>
<td>Ordovician (Katian)</td>
</tr>
<tr>
<td><em>Hybocrinus conicus</em> Billings, 1857</td>
<td>Hybocrinida</td>
<td>Ordovician (Sanbian)</td>
</tr>
<tr>
<td><em>Hybocystites problematicus</em> Wetherby, 1880</td>
<td>Hybocrinida</td>
<td>Ordovician (Katian)</td>
</tr>
<tr>
<td><em>Pentacrinites fossilis</em> Blumenbach, 1804</td>
<td>Articulata</td>
<td>Triassic (Anisian)</td>
</tr>
<tr>
<td><em>Porocrinus conicus</em> Billings, 1857</td>
<td>Porocrinida</td>
<td>Ordovician (Katian)</td>
</tr>
<tr>
<td><em>Rhodocrinites verus</em> Miller, 1821</td>
<td>Diplobathrida</td>
<td>Mississippian (Tournaisian)</td>
</tr>
<tr>
<td><em>Rosfacrinus robustus</em> LeMenn and Spjelknaes, 1996</td>
<td>Eucamerata</td>
<td>Ordovician (Katian)</td>
</tr>
<tr>
<td><em>Syndathocrinus conicus</em> Phillips, 1836</td>
<td>Disparida</td>
<td>Mississippian (Tournaisian)</td>
</tr>
<tr>
<td><em>Taxocrinus macrodactylus</em> (Phillips, 1841)</td>
<td>Flexibilia</td>
<td>Devonian (Famennian)</td>
</tr>
</tbody>
</table>

**Table 4.1**
Table 4.2 Revised rank-based classification of the Crinoidea. † indicates an extinct taxon.
Clas\ Class Crinoidea Miller, 1821

†Subclass Camerata Wachsmuth and Springer, 1885

‘Stem eucamerates’ (e.g., *Eknomocrinus*)

Infraclass Eucamerata Cole, in press

Order Diplobathrida Moore and Laudon, 1943

Order Monobathrida Moore and Laudon, 1943

Crinoidea *incertae sedis*: †Protocrinoidea Guensburg and Sprinkle, 2003

Subclass Pentacrinoidea Jaekel, 1894

†‘Stem inadunates’ (e.g., *Apektocrinus*)

Infraclass Inadunata Wachsmuth and Springer, 1885

†Parvclass Disparida Moore and Laudon, 1943

Order Eustenocrinida Ulrich, 1925

Order Maennilicrinida Ausich, 1998b

Order Tetragonocrinida Stukalina, 1980

Order Calceocrinida Meek and Worthen, 1869

Disparida *incertae sedis*: “Homocrinida” Kirk, 1914

Disparida *incertae sedis*: “Myelodactyla” S. A. Miller, 1883

Disparida *incertae sedis*: “Pisocrinoidea” Ausich and Copper, 2010

Parvclass Cladida Moore and Laudon, 1943

†Superorder Porocrinoidea Wright, in press

Order Porocrinida Miller and Gurley, 1894

Continued
<table>
<thead>
<tr>
<th>Order Hybocrinida Jaekel, 1918</th>
</tr>
</thead>
<tbody>
<tr>
<td>†Superorder Flexibilia Zittel, 1895 (<em>Cupulocrinus</em> d’Orbigny, 1849)</td>
</tr>
<tr>
<td>Order Taxocrinida Springer, 1913</td>
</tr>
<tr>
<td>Order Sagenocrinida Springer, 1913</td>
</tr>
<tr>
<td>Magnorder Eucladida Wright, in press</td>
</tr>
<tr>
<td>†Superorder Cyathoformes new superorder</td>
</tr>
<tr>
<td>Cyathoformes <em>incertae sedis</em>: “Cyathocrinida” Bather, 1899</td>
</tr>
<tr>
<td>Cyathoformes <em>incertae sedis</em>: “Dendrocrinida” Bather, 1899</td>
</tr>
<tr>
<td>Cyathoformes <em>incertae sedis</em>: “Poteriocrinida” Jaekel, 1918</td>
</tr>
<tr>
<td>Eucladida <em>incertae sedis</em>: †“Ampelocrinida” Webster and Jell, 1999</td>
</tr>
<tr>
<td>Superorder Articulata Miller, 1821</td>
</tr>
<tr>
<td>†Order Holocrinida Jaekel, 1918 Rasmussen, 1978</td>
</tr>
<tr>
<td>†Order Encrinida Matsumoto, 1929</td>
</tr>
<tr>
<td>†Order Millericrinida Sieverts-Doreck, 1953</td>
</tr>
<tr>
<td>†Order Uintacrinida Zittel 1879</td>
</tr>
<tr>
<td>†Order Roveacrinida Sieverts-Doreck, 1953</td>
</tr>
<tr>
<td>Order Cyrtocrinida Sieverts-Doreck, 1953</td>
</tr>
<tr>
<td>Order Hyocrinida Rasmussen, 1978</td>
</tr>
<tr>
<td>Order Isocrinida Sieverts-Doreck, 1953</td>
</tr>
<tr>
<td>Order Comatulida A. H. Clark, 1908</td>
</tr>
</tbody>
</table>
Figure 4.1 Taxa representing major crinoid clades: (1) *Pentacrinites fossilis* Blumenbach, 1804, articulate, from Goldfuss (1831); (2) *Taxocrinus colletti* White, 1881, flexible, from Springer (1920); (3) *Actinocrinites jugosus* (Hall, 1859), monobathrid camerate, from Wachsmuth and Springer, 1897; (4) *Synbathocrinus swallowi* Hall, 1858, disparid, from Wachsmuth and Springer (1897); (5) *Dendrocrinus caduceus* Hall, 1866, eucladid, from Meek (1873); (6) *Hybocystites eldonensis* Parks, 1908, hybocrinid, from Springer (1911); (7) *Porocrinus shawi* Schuchert, 1900, porocrinid, from Kesling and Paul (1968); (8) *Archaeocrinus microbasalis* (Billings, 1857), diplobathrid camerate, from Wachsmuth and Springer (1897). All scale bars 0.5 cm and applicable as indicated.
Fig. 4.1
Figure 4.2 Cladogram depicting phylogenetic relationships among species used to define major clades within the Crinoidea. Terminal tips correspond to species listed in Table 1. Clades given stem-based definitions are indicated with a downward facing arrow, whereas clades given node-based definitions are indicated with a circle. Note that many clades named are nested inside other more inclusive clades. Graphical notation of stem- and node-defined clades follows Sereno (2005).
Fig. 4.2
Chapter 5: Ecologic innovation and phenotypic constraint in the evolutionary radiation of Paleozoic crinoids

Abstract.—Evolutionary radiations are one of the most discussed features in the history of life. The patterns and processes underlying phenotypic diversification during such radiations have been much debated by both paleontologists and comparative biologists. In this chapter, I take advantage of recently developed methods to test the relationships between phylogeny-based rates of morphologic evolution, taxonomic diversification, and morphospace occupation in the ~200 million year evolutionary radiation of Paleozoic crinoids. Focusing on the Eucladida, I find evidence for highly heterogeneous evolutionary dynamics, including variation in morphologic rates and shifts in evolutionary mode. The early history of eucladid diversification is characterized by “early burst” dynamics, but a late Paleozoic peak in morphologic rates is not associated with the diversification of a rapidly radiating subclade. Instead, the late peak in rates likely involved multiple smaller radiations linked to ecologic change. Results indicate phenotypic diversification is more complex than models commonly assumed in comparative biology, at least over geologic timescales—highlighting the need for continued synthesis between fossil and phylogenetic approaches to macroevolution.
Introduction

“How fast, as a matter of fact, do animals evolve in nature?” –G.G. Simpson (1944)

It is often stated that the major features of Earth’s biodiversity are the result of successive evolutionary radiations spanning the geologic history of life (Simpson, 1953). Adaptive radiation, a process whereby species rapidly diverge from a common ancestor and increase in phenotypic disparity as a result of ecologic opportunity, is the most commonly invoked type of evolutionary radiation and is backed by a rich theory and wealth of empirical case studies (Simpson, 1953; Schluter, 2000; Erwin, 2007; Losos, 2010). Adaptive radiation theory predicts that rates of phenotypic evolution are initially high during the early stages of radiation, such as when a lineage enters a new adaptive zone, but subsequently decline as a clade ages because niche space becomes saturated (Simpson, 1953; Schluter, 2000). A corollary of this prediction is that variation in morphologic disparity should peak early in a clade’s history. A possible alternative explanation to adaptive radiation is that a clade may achieve early maximum disparity for reasons not related to ecologic opportunities, but because phenotypic diversification was later limited by developmental constraints or time-heterogeneous selective pressures (Wagner, 1996, 2000; Erwin, 2007). Nevertheless, patterns of so-called “early burst” (Harmon et al., 2010) diversifications are commonly observed in paleontologic data (Foote, 1994, 1999; Erwin, 2007; Wagner, 2010; Hughes et al., 2013; Oyston et al., 2015), and recent radiations of well-studied living clades are broadly consistent with
predictions from adaptive radiation theory (Baldwin and Sanderson, 1998; Grant and Grant, 2002). In contrast with the fossil record, phylogenetic comparative data rarely support the early burst model and instead suggest that instances of evolutionary radiation are more frequently characterized either by patterns of constrained diversification around an adaptive peak or random diffusion through morphospace (Harmon et al., 2010). Although the lack of support for adaptive radiation in comparative data may reflect difficulties in testing early burst models (Harmon et al., 2010; Slater et al., 2010; Slater and Pennell, 2014), it nevertheless highlights the need to consider alternative models of phenotypic diversification associated with evolutionary radiations (Erwin, 1992; Simões et al., 2015) (Fig. 1).

For the last several decades, paleobiologists have tested conceptual models of radiation patterns by measuring temporal variation in morphologic disparity in fossil lineages (Foote, 1992, 1997; Erwin, 2007; Wagner, 2010). Disparity profiles are then compared with concomitant trends in taxonomic diversity to determine which alternative model best fits the observed trends (Foote, 1997; Jablonski, in press). A common assumption is that fluctuations in disparity primarily reflect underlying rates of morphologic change. Although this prodigious research program has generated important insights into patterns of morphologic diversification (Wagner, 2010), such as whether the high early disparity patterns observed in the fossil record are consistent with ecologic processes or other mechanisms (Foote, 1997; Erwin, 2007), there are several causes for concern as to whether or not disparity measures provide a general context for inferring phenotypic rates of evolution. For example, alternative evolutionary processes with
strikingly different rates of morphologic evolution can yield equivocal disparity profiles (Foote, 1996; Slater, 2015). Moreover, even under simple models of trait evolution, such as Brownian motion, sister clades with different rate dynamics may theoretically obtain identical disparities because of the way trait variation is partitioned among subclades (O’Meara et al., 2006). Thus, assessing the rate of morphologic evolution requires the explicit use of phylogenetic trees (Foote, 1996). When combined with time-calibrated phylogenies, disparity estimates can more explicitly be used to test relationships between rates of change and morphospace occupation (Wagner, 1997).

This chapter takes advantage of recently developed phylogeny-based methods to test two questions pertinent to how diversification trajectories unfold over geologic time. Using the fossil record of Paleozoic eucladid crinoids (Echinodermata), I test whether their ~200 million year radiation exhibits temporal dynamics predicted by adaptive radiation theory. I then compare per-lineage-million-year rates of character change with patterns of morphospace occupation to test whether morphologic evolution was driven primarily by ecologic opportunities, innovation, or phenotypic constraints. The Eucladida (Wright, in press) are a major clade of crinoids and provide a model system for addressing these questions. Eucladids are both ecologically and taxonomically diverse (Webster, 2013), and are characterized by a well sampled fossil record (Foote and Raup, 1996; Foote and Sepkoski, 1999). Importantly, fossil crinoids preserve morphologic features useful for inferring evolutionary relationships from phenotypic data (Wright et al., in press) and their exoskeleton can be compared with living species to infer feeding ecology and life history (Ausich, 1980; Kitazawa et al., 2007; Kammer, 1985, 2008).
These features make fossil crinoids ideal for testing relationships between patterns of morphologic diversification and adaptive zone occupation, as well as evaluating ecologic differences among species shape evolutionary radiations over geologic timescales.

**Results and Discussion**

Rates of morphologic evolution for Ordovician through Permian eucladids were calculated using 92 discrete morphologic traits spanning the entire eucladid body plan. Two phylogeny-based methods were used. The first method divides the number of character changes occurring within ~7 million year bins by the sum of within-bin branch length durations and uses likelihood ratio tests to infer whether intervals are characterized by statistically elevated or depressed rates. The second method estimates the median percent amount of character change per million years using a Bayesian relaxed morphologic clock model. Although recent work has illuminated phylogenetic relationships among crinoids (Ausich et al., 2015; Cole, in press; Wright, in press; Wright et al., in press), the phylogeny of Paleozoic eucladids remains elusive, and they have not received comprehensive systematic treatment since publication of the crinoid *Treatise* (Moore et al., 1978). A phylogenetic analysis of a morphologic character matrix coded for 81 species did not recover any of the order-level taxa listed in the crinoid *Treatise* (Moore et al., 1978). However, the validity of these orders has long been questioned and results are broadly consistent with previous taxonomic recommendations (McIntosh,
The maximum clade credibility (MCC) tree resulting from a Bayesian analysis using a relaxed morphologic clock and a time-varying fossilized birth-death process (FBD) tree prior is well resolved near the base of the tree, but elsewhere characterized by low support (see Materials and Methods section). To account for uncertainties in evolutionary relationships and divergence times, all rate analyses were performed over random samples of time-calibrated trees from the Bayesian posterior distribution.

Both maximum likelihood and morphologic-clock methods reveal major fluctuations in the rate of morphologic evolution for eucladid crinoids across the Paleozoic (Fig. 5.2). Morphologic rates for Paleozoic eucladids were at their highest early in the clade’s history and exhibit a long-term secular decrease in mean rates of evolution through time (Spearman’s $Rho = -0.46$, $P = 0.022$). The Late Ordovician to middle Silurian is characterized by elevated rates of character change that are approximately twice as high as most subsequent intervals of the Paleozoic. Rates significantly drop during the Devonian, reaching their Paleozoic minimum during the Frasnian-Famennian stages. Although rates modestly increased during the early Carboniferous, they do not rise above background levels and are comparable to those of the late Silurian to early Devonian. Rates were elevated throughout much of the late Carboniferous (Bashkirian-Kasimovian), with a burst of morphologic evolution occurring during the Moscovian stage that resulted in the only significant post-Silurian peak in morphologic rates (Fig. 5.2). Although the early to middle Paleozoic radiation of eucladids is consistent with an
“early burst” type pattern, the episodic peak during the late Carboniferous suggests morphologic diversification during the late Paleozoic was driven by different evolutionary dynamics.

It is important to rule out possible biases that may influence these patterns because variation in rate estimates can arise even when underlying rates of evolution are constant. For example, elevated rates of evolution may be inferred simply because taxa were more densely sampled and therefore more changes can be recorded. However, a phylogeny-based diversity curve (Fig. 5.3, [lower figure]) shows a major peak during the early Carboniferous, which is not associated with high rates of change. Similarly, diversity was much lower during the Ordovician to middle Silurian than most of the Paleozoic. A comparison of the phylogeny-based diversity of sampled lineages with the number of all known valid eucladid genera reveals late Carboniferous eucladids are proportionally undersampled in the dataset (Webster, 2013) (Fig. 5.3 [cf. middle and lower figures]). Thus, the late Carboniferous peak in morphologic rates would be expected to be even higher if species had been sampled in proportion to taxonomic richness.

Sampling biases arising from incompleteness of the fossil record could also affect rate estimates. Paleontologic metrics assuming uniform preservation (Foote and Raup, 1996) indicate sampling probabilities for Paleozoic eucladids are slightly higher than estimates for all Ordovician to Devonian crinoid genera (per-interval preservation probability = 0.60, sampling rate = 0.12) (Foote and Raup, 1996) suggesting the eucladid record is ~92% complete when evaluated at the family level. Crinoids as a whole exhibit
different post-mortem disarticulation rates (Meyer et al., 1989), but patterns of
taphonomic degradation are similar within major clades such as the Eucladida (Ausich et
al., 1999). Thus, there is no a priori reason to suspect substantial variation in preservation
potential among taxa analyzed. However, non-uniform preservation of the rock record
itself may also influence paleontologic patterns, especially over geologically long
timescales ($10^7$-$10^8$ years) (Holland, 2016). A stochastic model of non-uniform sampling
was incorporated directly into the phylogenetic analysis and used to estimate time-
varying rates of fossil sampling (see Materials and Methods). Although sampling
fluctuated through time (Fig. 5.4C), there is a nonsignificant correlation between
sampling rate and inferred rates of character change (Spearman’s $Rho = 0.155$, $P =
0.459$). In summary, the inferred rates of morphologic evolution are robust to a number of
potential biases that may affect rate inferences, including variation in tree topology,
branch lengths, divergences times, and incomplete or non-uniform fossil sampling.

Other phylogeny-based disparity studies with paleontologic perspectives have
suggested that bursts of morphologic change occurring after a clade’s early history are
associated with major ecologic shifts and diversification of one or more subclades (Slater,
2012, 2015; Close et al., 2015; Hopkins and Smith, 2015). Feeding ecology is the
primary control on niche differentiation among crinoids (Ausich, 1980; Kitazawa et al.,
2007). Crinoids are passive suspension feeders that depend on the current-driven nutrient
supply to feed and have evolved a variety of ecomorphologic traits to help capture food
particles and reduce competition among species (Ausich, 1980; Kitazawa et al., 2007;
Baumiller, 2008). Two eucladid subclades, cyathoform and cladoform crinoids (sensu
Kammer and Ausich, 1992, 1996; Webster, 2012), represent different functional groups and are each strongly supported as monophyletic (posterior probability = 1) (see Materials and Methods) (Fig. 5.2). Although cyathoform and cladoform species often co-occur in the same paleocommunities (e.g., on the same bedding plane), they are characterized by traits reflecting adaptations to different ecologic and environmental conditions (Ausich, 1980; Kammer, 1985, 2008). Cladoform crinoids have terminal arm appendages called pinnules that serve to increase filtration fan density, which allows for feeding to take place at higher current velocities (Kammer, 1985). In addition, cladoforms have muscular appendages in the arms that increase motility and enable shifts in feeding posture (Kammer, 1985; Baumiller and Messing, 2007). In contrast with cladoforms, cyathoform crinoids almost universally lack pinnules and have ligamentary articulations with limited motility.

The early history of eucladid evolution predominantly reflects patterns of cyathoform diversification. The cyathoform subclade is characterized by deaccelerating rates through time (Spearman’s $Rho = -0.930, P < 0.001$) (Fig. 5.5), consistent with expectations of an early burst model. In contrast, variation in rates after the Devonian is most strongly associated with cladoforms. A small rise in rates is coincident with the gradual assembly of the cladoform body plan during the Devonian (Fig. 5.2), and rates of change within the subclade are higher early in their history than in subsequent intervals (Fig. 5.5). However, long-term rates of change among cladoforms show no evidence for a secular trend (Spearman’s $Rho = 0.042, P = 0.873$), and the highest rates of evolution occur much later in their history (Fig. 5.5). Thus, rates of morphologic evolution
characterizing cladoform diversification do not support an early burst pattern of phenotypic diversification despite substantial ecomorphologic innovation.

Major trends in crinoid evolution have been attributed to long-term effects of biotic interactions and/or species ecology (Meyer and Macurda, 1977; Baumiller, 1993; Ausich et al., 1994; Kammer and Ausich, 2006; Sallan et al., 2011; Gorzelak et al., 2015). The pattern of shifting subclade contributions to the broader eucladid radiation is consistent with paleoecologic observations regarding ecologic abundance, taxonomic diversity, and turnover between these groups (Ausich et al., 1994). Thus, the ecologic differences between cladoform and cyathoform eucladids may have resulted in different macroevolutionary dynamics. Indeed, background rates of morphologic evolution are higher among cladoforms than cyathoforms (Mann-Whitney U test, \( W = 231, P < 0.001 \)).

It is possible that higher rates in cladoform eucladids may have resulted from increased competition with other pinnulate crinoid clades (e.g., camerate) that share similar functional ecologic traits. However, eucladids and camerate crinoids broadly differ in their habit preferences (Kammer and Ausich, 2006), which suggests elevated rates of morphologic evolution in cladoform eucladids were driven by processes other than (or in addition to) competition. Similarly, the rate of adaptive phenotypic evolution is expected to be greater in clades experiencing increased predation pressure (Vermeij, 1987). Increased predator-prey dynamics have previously been linked with macroevolutionary patterns in Paleozoic crinoids (Signor and Brett, 1984; Sallan et al., 2011), but a comparison of diversification trajectories found no significant relationship between eucladids and their probable vertebrate predators (Sallan et al., 2011). Lastly,
higher rates for cladoform eucladids may have resulted from environmental factors that influence ecologic specialization, which has been linked with higher rates of evolution (Vrba, 1987). Baumiller (1993) found evidence for higher rates of taxonomic diversification for camerate crinoids with more finely-filtered fan morphologies and attributed the pattern to long-term stenotopic effects on diversification. Although cladoforms also have dense filtration fans, the evolution of muscular articulations in their arms facilitated a greater range of feeding postures that led to cladoforms being able to inhabit a broader range of environments than other crinoid lineages (Baumiller, 1993; Holterhoff, 1997). Thus, stenotopy in eucladids is not easily equated with stenotopy in other crinoids. The concept of evolution occurring within adaptive zones (Simpson, 1953) provides a possible explanation. If cladoforms occupied a broader adaptive zone than cyathoforms, then evolution within subzones (Simpson, 1953) would lead to ecologic specialization and increased rates of phenotypic change in cladoform subclades.

A morphospace analysis of the complete character matrix shows disparity within cladoform eucladids is much greater than among cyathoforms (Fig. 5.6), especially when patterns of morphospace occupation are evaluated over time (Fig. 5.7). Cyathoform eucladids rapidly expanded in morphospace during their explosive Ordovician-Silurian radiation and reached their maximal disparity during the Silurian. Although cyathoforms continued to diversify throughout the Paleozoic, they never expanded into new regions of morphospace outside those that originally evolved during the early Paleozoic. Thus, the early history of cyathoform evolution is consistent with an early burst-type pattern and with expectations from adaptive radiation theory. However, their subsequent
diversification during the middle to late Paleozoic is more consistent with increased constraints on morphologic evolution that limited expansion into previously unexplored regions of morphospace.

In contrast, cladoform eucladids expanded in disparity during the Devonian and reached peak morphologic diversity during the Mississippian, occupying vast regions of morphospace spanning multiple Simpsonian subzones (Figs. 5.6-5.7). The distribution of eucladids in morphospace was highly asymmetric during the Pennsylvanian, as the advanced cladoform subzone became saturated and very few regions outside this zone were occupied. However, the advanced cladoform cluster diminished in importance by the Permian. Cyathoforms and intermediate zone cladoforms re-radiated into pre-explored regions of morphospace, whereas extinction of closely spaced taxa occurred within the advanced cladoform zone. The broad distribution in eucladids in morphospace coupled with extinction of intermediate forms ultimately led to the Permian being the time of maximal morphologic disparity in the Paleozoic radiation of eucladids (Fig. 5.3).

The preceeding discussion has focused on rates of morphologic evolution and overall trends in morphospace occupation through time. However, most theoretical models describing the dynamics of evolutionary radiations also make predictions about patterns of taxonomic diversification (Rabosky and Adams, 2012; Jablonski, in press). Taxonomic diversification is an exponential process, whereas morphologic diversification is approximately linear under constant rate Brownian motion assumptions (Foote, 1996). If taxonomic diversity is plotted on a log scale in diversity-disparity space, then exponential taxonomic diversification coupled within a Brownian motion-like
diffusion process for morphologic evolution would predict a linear fit between diversity and disparity measures (Jablonski, in press).

The relationship between morphologic disparity and taxonomic diversity in the radiation of Paleozoic eucladids is depicted in Figure 5.8. Diversity and disparity both rapidly increase from the Ordovician through the Devonian and rise significantly above the 1:1 diagonal (Fig. 5.3 (upper), Fig. 5.9). Likelihood ratio tests confirm that rates of morphologic evolution were high throughout the Ordovician to early Silurian (Fig. 5.2), with high rates accompanying the rapid expansion of cyathoform eucladids in morphospace. When coupled with the concomitant rise in taxonomic diversity during this interval, these patterns suggest the early history of eucladid radiation was characterized by an early burst-like model of morphologic evolution and is consistent with adaptive radiation theory. The end-Ordovician extinction dramatically altered the structure of crinoid communities (Ausich et al., 2004), but it is not clear how the extinction may have affected eucladid diversification. Net taxonomic diversification fell dramatically during the end Ordovician (Fig. 5.4), but the overall diversity trajectory for eucladids shows a nearly constant rate increase from the Ordovician through the end of the Silurian (Fig. 5.3). It is possible the end-Ordovician extinction played a role in sustaining rates of morphologic evolution for such geologically long intervals. For example, the opening of niche space that followed the end-Ordovician may have allowed their early Paleozoic radiation to continue in a protracted diversification. Alternatively, the extinction event may have led eucladids to undergo a post-extinction adaptive radiation and the observed geologically sustained rates may reflect two contiguous diversification events.
Post-Silurian dynamics reveal more complex patterns. Despite significant expansion into new regions of morphospace that correspond to the initial radiation of cladoforms during the Devonian (Fig. 5.7), the rise in disparity was not accompanied by a significant increase in morphologic rates. Instead, rates of morphologic evolution do not differ significantly from background for much of the Devonian. Further, the Late Devonian marks the only interval in eucladid diversification with evidence for significantly low rates of character change (Fig. 5.2). Thus, morphologic innovation associated with the assembly of the cladoform body plan did not result in an “early burst”-like peak corresponding with the origination of the clade (Hopkins and Smith, 2015). Instead, morphologic diversification from the Devonian to early Carboniferous is more similar to a Brownian motion-like process. Brownian motion diffusion through morphospace would be expected to result in increased disparity even if morphologic change was occurring at a low, constant rate. This suggests the Devonian increase in morphologic disparity should not be interpreted as high underlying rates of change, but instead as a fundamental shift in the underlying mode of evolution.

The early Carboniferous (Mississippian) features a dramatic increase in taxonomic diversity, marking the so-called “Age of Crinoids” (Kammer and Ausich, 2006) (Figs. 5.3, 5.8). Notably, taxonomic diversification among eucladids was most dramatic among cladoforms during this interval (Kammer and Ausich, 2006). The macroevolutionary lag (Jablonski, 2008) between the assembly of the cladoform body plan and subsequent taxonomic diversification may be explained, in part, by the late Devonian global collapse of reefs. The demise of coral-stromatoporoid dominated reefs
facilitated a major environmental transition from abundant, more restricted rimmed carbonate platforms to widespread open ramp settings in epicontinental seas, resulting in a substantial increase in habitat space favorable for crinoids (Kammer and Ausich, 2006). Global geographic expansion of eucladids during the Mississippian may have led to increased speciation propensity (Simões et al., 2015), resulting in a substantial net increase in taxonomic diversification (Kammer and Ausich, 2006). Although disparity slightly increased during the Mississippian, morphospace became more tightly clustered in cladoform zones. Rates of evolution may have continued to follow a Brownian motion-like process, but with an increasing role for constraint in morphologic diversification rather than unbounded diffusion in morphospace.

The rise in morphologic rates of evolution during the late Carboniferous (Pennsylvanian) is coincident with a similar rise in taxonomic diversity (Figs. 5.2-5.3), culminating in both maximal genus-level diversity and the only post-Silurian rate peak supported by likelihood ratio tests during the Middle Pennsylvanian. However, the Pennsylvanian did not exceed the Mississippian in net taxonomic diversification, which suggests the diversity peak is a result of increased taxonomic longevity rather than elevated origination (Fig. 5.4). Episodic, elevated rates can result from early burst like patterns of adaptive radiation within a single lineage (Hopkins and Smith, 2015; Slater, 2015). Examination of rates inferred on the MCC from the Bayesian morphologic clock analysis tree instead reveals multiple lineages were evolving at high rates during the Pennsylvanian (Fig. 5.2). Interestingly, the Pennsylvanian is associated with an overall decrease in disparity despite the elevated rates of character change (Fig. 5.8).
Diversification during the Pennsylvanian was dominated by taxa within a narrow region of morphospace contained within the advanced cladoform subzone (Fig. 5.7). The centripetal direction of changes implied by the MCC phylomorphospace indicates morphologic diversification was highly constrained within the cladoform subzone.

That multiple clades were rapidly evolving similar morphologies is suggestive of a shared response to similar ecologic or selective pressures. For example, Paleozoic eucladids exhibit a temporal trend in the calyx plates in pinnulate eucladids. This trend is best expressed in Carboniferous eucladids and is correlated with a reduction in body size (Kammer, 2008). These trends may reflect an adaptive paedomorphic response to rapidly fluctuating environmental conditions and increased sediment disturbance (Kammer, 2008; Wright, 2015). Thus, morphologic evolution during the Pennsylvanian is suggestive of another major shift in underlying evolutionary mode. Constrained diversification within a limited, circumscribed region of morphospace is consistent with a macroevolutionary Ornstein-Uhlenbeck (OU) model of morphologic evolution. Although phenotypic optima for an OU-like dynamic may have theoretically existed any time after the advanced cladoform zone became available, the evolutionary attractor driving bounded morphologic evolution during this interval was much stronger than any time before or after the Pennsylvanian. This and other instances of replicate radiations within Simpsonian subzones, such in fossil canids (Slater, 2015b), strongly suggests that adaptive evolution may result in patterns of constrained phenotypic diversification during instances of ecologic radiation (Erwin, 1992).
If these results can be generalized to apply to other clades, then the extreme heterogeneity observed in Paleozoic eucladid evolution strongly suggests that commonly used models of phenotypic diversification (Fig. 5.1) do not adequately capture the dynamics of evolutionary radiations, at least those occurring over long timescales. In addition, paleontologic inferences from studies of disparity through time may be misled if a strong relationship between rates of evolution and morphospace occupation is assumed. Rather than dismay over challenges presented, I advocate that where possible, the data and methods of both fields be combined and synthesized to help better understand the pattern and process in macroevolutionary biology. This study highlights how integrating phylogeny-based estimates of morphologic evolution with traditional paleontologic measures of disparity provides a more nuanced understanding of phenotypic diversification, especially during major radiations spanning vast amounts of geologic time.

**Materials and Methods**

*Morphologic and stratigraphic data*

I compiled a data matrix of 92 morphologic characters for 81 species of Paleozoic eucladid crinoids and one outgroup (Appendix A). The majority of characters included overlap with Wright (in press), but I excluded any characters with invariant distributions among sampled taxa and included new characters (and character states) to accommodate
morphologic variation in middle to upper Paleozoic eucladids. The Eucladida (Wright, in press) range from the Ordovician (Katian) to the present (Wright et al., in press), and their Paleozoic fossil record includes more than 500 genera (Webster, 2013). To obtain an analytically tractable sample of species for analysis, representative species were chosen from nominal families (Moore et al., 1978; Webster, 2013) to capture broad taxonomic, morphologic, and preservational gradients among taxa. In most cases, species sampled were type species of a type genus. However, some geologically older species were sampled, especially when an older species was represented by more completely preserved specimens and was available for coding. All missing or inapplicable characters were coded as “?” (~20% of the cells). The mean number of unscored cells per taxon (18.2%) and per character (16.5%) are both relatively low and similar to one another. Thus, taxonomic and character-based biases introduced by missing data are likely minimal for this dataset. Notably, this dataset is more complete than comparable studies testing phylogeny-based rates of morphologic evolution over geologic timescales (e.g. Close et al., 2015; Hopkins and Smith, 2015).

Although the character list was constructed primarily for use in phylogenetic analysis, it is also amenable for studying character-based morphologic disparity. A comparison of disparity metrics using cladistic matrices of discrete characters indicates cladistic data are often good proxies for summarizing morphologic variation (Hetherington et al., 2015), and a number of empirical studies use cladistic matrices for testing general hypotheses of morphologic evolution (Close et al., 2015; Hopkins and Smith, 2015; Lloyd, 2016). Autapomorphies are often excluded from phylogenetic
datasets because they are not parsimony-informative (i.e., they have the same length on all trees), but are included in disparity studies because they contribute to the total variation in morphologic form. However, this study includes parsimony-informative characters and a small number of autapomorphies. The inclusion of autapomorphies in model-based (i.e., probabilistic) phylogenetic analyses may improve phylogenetic inferences via more accurate estimation of branch lengths and rates of change (Lewis, 2001). Characters were coded by examining specimens housed in museum collections, including the Smithsonian Institution, Field Museum of Natural History, the Natural History Museum (London), and the Lapworth Museum of Geology. Most species were coded using multiple specimens, such as types and paratypes in their type-series. Additional data was collected by examining the primary taxonomic literature.

All numerical dates and names for geologic intervals are taken from the 2016 International Chronostratigraphic Chart (Cohen et al., 2013, updated). Stratigraphic data constraining species temporal ranges were obtained from an updated version of Webster (2013). Most analyses consist of data binned to the stage-level and range from the Ordovician (Katian) to Permian (either the Wordian or Wuchiapingian depending on the analysis). However, Silurian data was binned according to the series-level in an attempt to make the temporal duration between time bins more comparable and reduce difficulties in fine-scale stratigraphic correlation when assigning fossil occurrence dates (see Webster, 2013). Following Cohen et al. (2013), the Carboniferous Period was subdivided into subperiods: the early Carboniferous (Mississippian) and late Carboniferous (Pennsylvanian).
Phylogenetic analysis

To obtain a distribution of time-calibrated phylogenies, I used a Bayesian fossil tip-dating approach as implemented in MrBayes 3.2.6 (Ronquist et al., 2012). A Markov model of character evolution (Lewis, 2001) was used with character coding set to variable and a 4-category gamma distribution was applied to account for rate variation among characters. All characters were treated as unordered. Rate variation among lineages was estimated using the uncorrelated, independent gamma rates (IGR) relaxed morphologic clock model (Lepage et al., 2007), with a broad exponential hyperprior (λ = 10) on the variance of the gamma distribution. A truncated Gaussian prior was placed on the base rate of the clock (mean = 0.01, standard deviation = 0.1).

The time-varying (piecewise-constant) skyline implementation of the sampled ancestor fossilized birth-death process (SA-FBD) was used as a prior distribution on branch lengths (Heath et al., 2014; Gavryushkina et al., 2014; Zhang et al., 2016; Wright, in press). Thus, SA-FBD parameters were estimated across broad geologic intervals, corresponding to the Late Ordovician-Silurian, Devonian, Mississippian, and the Pennsylvanian-mid Permian. For each interval, SA-FBD parameters were assigned an exponential prior (λ = 10) on net diversification, a flat (Beta[1,1]) prior on relative extinction, and a Beta(2,2) distribution on fossil sampling. Because taxon sampling is highly incomplete at the species-level but broadly covers all major eucladid higher taxa, the diversified sampling correction of Zhang et al. (2016) was applied. The proportion of ‘extant’ species sampled at the end of the SA-FBD process was set to 0.008, which is
based on the assumption that middle to late Permian crinoid species diversity was at least as high as that of today (Donovan et al., 2016).

Bayesian fossil tip-dating requires information on the temporal ages and/or ranges of fossil samples (Gavryushkina et al., 2014; Wright, in press). Preliminary tip-dating analyses had difficulty converging (according to MrBayes diagnostics) when species occurrences were assigned uniform distributions according to the duration of their first appearing stages in Webster (2013). However, convergence was more easily reached when point occurrences were used. Because data is lacking for precise numerical estimates of species first-appearances (Webster, 2013), the mid-point of the time bin for each species’ first appearance was used as a point constraint on occurrence times. Based on both stratigraphic and phylogenetic evidence, the split between Eucladida and their nearest outgroup occurred during the earliest part of the Katian stage of the Ordovician (Webster, 2013; Wright, in press). Thus, the tree age prior was set to correspond to an early Katian divergence.

To assist the analysis, a series of partial and hard topological constraints based on results of Wright (in press) were applied. Maximum parsimony and topology-only Bayesian analyses (using PAUP* [Swofford, 2002] and MrBayes) were used to identify additional sets of taxa that could be constrained, and clades recovered by both analyses were given partial constraints. Two Markov chain Monte-Carlo runs with four chains were run for 30 million generations, sampling trees every 3000 steps. MCMC convergence was assessed using methods described in chapter 3 and 50% of the samples were discarded as burn-in, resulting in a posterior distribution of 5,000 time-calibrated
phylogenetic trees. The maximum clade credibility tree (MCC) depicting the posterior probability of nodes and 95% highest density probability for divergences are presented in Figure 5.2.

*Rates of morphologic evolution*

Rates of character change were inferred using two methods: a maximum-likelihood approach that estimates rates of character changes occurring along branches of time-calibrated trees (Lloyd et al., 2012), and a Bayesian relaxed morphologic clock analysis in MrBayes (Ronquist et al., 2012).

Lloyd et al. (2012) developed a novel approach to estimated rates of morphologic evolution in a likelihood framework that accounts for the effect of missing data, which was later refined by Brusatte et al. (2014) and Lloyd, 2016. This method models character changes as a Poisson process with a rate parameter \( \lambda_i \) and uses likelihood ratio tests to identify intervals with significantly high or low rates of evolution. Ancestral states at internal nodes are first estimated for all comparable characters from time-calibrated phylogenies using maximum likelihood (Lloyd, 2016), and then rates of morphologic evolution are calculated as the number of changes occurring along a branch (i.e., number of parsimony steps) divided by the product of time (measured in millions of years) and completeness (measured as the proportion of the observed comparable characters). Following Lloyd et al. (2012), let \( X_i \) denote the number of character changes occurring in the \( i^{th} \) interval, \( c_i \) is completeness, and \( t_i \) represents the temporal duration of a
time bin in millions of years. Thus, the probability of observing $x$ character changes is given as (Lloyd et al., 2012)

$$P(X_i = x|\lambda_i) = \frac{e^{-\lambda_i} (\lambda_i t)^x}{x!}.$$  

Likelihood ratio tests (LRT) are used to test whether $\lambda$ for given time bin is significantly high or lower than $\lambda$ estimated from the remaining pooled bins. The significance level $\alpha$ for LRTs was set to 0.01. The Benjamini-Hochberg test was used to correct for multiple comparisons and their associated type I errors (Benjamini and Hochberg, 1995; Lloyd et al., 2012). Because the rates inferred from this method are sensitive to the tree topology and branch lengths, I calculated rates of evolution over a random sample of 100 trees from the Bayesian posterior distribution of time-calibrated trees. Thus, the results are robust across many alternative hypotheses of evolutionary relationships and node age estimates. If a time bin contained >55% of rate estimates with statistically significant (i.e., $P < 0.01$) high or low values across the posterior sample of trees, it was regarded as having rates significantly different from background.

Rates inferred using a Bayesian relaxed morphologic clock were estimated in MrBayes 3.2.6 (Ronquist et al., 2012) using the same prior distribution settings described above for phylogenetic analysis. To account for uncertainty, percent character changes per million years were obtained by taking the median values of rates sampled in the Bayesian posterior distribution of trees. Time-calibrated branch lengths and rates of evolution are estimated simultaneously. It should be noted that recovery of time-
heterogeneous rate dynamics using this approach runs opposite of methodological biases because it assumes morphologic evolution can be fit to a clock-like model (Lloyd, 2016).

**Standing diversity and diversification rates**

Taxonomic diversity and taxonomic rates of origination and extinction were estimated from data contained within a recently updated compilation of 505 genus-level eucladid occurrences spanning the Paleozoic (Webster, 2013). Where appropriate, I modified the data listed in Webster (2013) to update stratigraphic correlations and alpha taxonomy. Generic diversity was estimated using the first and last appearances recorded by Webster (2013) with the common range-through assumption (Foote and Miller, 2007). Uncertainty in the number of genera occurring per bin was estimated using a Monte-Carlo analysis consisting of 1,000 bootstrap replicates.

Per-capita rates of taxonomic diversification were estimated using equations presented in Foote (2000) for tabulations of biostratigraphic ranges and is based on the assumption of exponential survivorship (Raup, 1985). The extinction rate is calculated as the proportion of taxa alive at the start of an interval that survived at least to the end of the interval. Thus, the extinction rate is \( q = \frac{-\ln[(N_{bt}) / (N_b)]}{\Delta t} \), where \( q \) is the extinction rate per-lineage-million years, \( N_{bt} \) is the number of taxa that cross both the beginning and end of the interval, \( N_b \) is the number of taxa that cross the bottom boundary, and \( \Delta t \) is the temporal duration of the interval in units of \( 10^6 \) years. Similarly, the origination rate is based on the proportion of taxa present at the end of an interval that already existed prior to the beginning of the interval. The per-lineage-million year origination rate is calculated
as \( p = -\ln\left(\frac{N_{ht}}{N_t}\right) / \Delta t \), where \( p \) is the origination rate, \( N_t \) is the number of taxa crossing the top boundary, and other terms are the same as described above. Net taxonomic diversification per interval is simply \( p - q \), and taxonomic turnover is \( q/p \) (Fig. 5.4). Although improved analytical methods exist to estimate standing diversity and taxonomic diversification (e.g., Alroy, 2010, 2016), these approaches require detailed information on fossil occurrences rather than tabulation of first and last appearances. Discipline-based efforts to compile such data exist (e.g., paleobiodb.org). However, at present these databases do not have sufficient taxonomic and temporal coverage to satisfy the requisite data needed to implement occurrence-based approaches. Nevertheless, the taxonomic rates presented herein represent estimates based on the most comprehensive, taxonomically vetted dataset of eucladid crinoids ever compiled and stratigraphic range-based methods often provide a good proxy for diversification dynamics (Foote, 2000; Peters and Ausich, 2008).

In addition to taxonomic rates, the time-series of SA-FBD parameters estimated during phylogenetic analysis can also be used to infer diversification dynamics and compared with paleontologic estimates. These parameters are summarized in Figure 5.4. Although differences exist between taxonomic and SA-FBD estimates (e.g., the SA-FBD represent coarse scale averages whereas the finer resolution taxonomic rates are subject to sampling biases [see Alroy, 2010]), broad pattern trajectories are similar when paleontologic estimates are averaged over timescales comparable with FBD estimates (Fig. 5.4). For example, the median rate of taxonomic turnover for the Devonian Period is 0.73, which is close to the SA-FBD estimate of 0.71.
Phylogenetic standing diversity was calculated as the median diversity across 500 randomly sampled time-calibrated trees from the posterior distribution (Bapst, 2012). Uncertainty around the median was characterized using two-tailed 95% upper and lower quantiles (see Bapst, 2012).

*Morphologic disparity and morphospace occupation*

Morphologic disparity was calculated as the average squared distance between species in morphospace, which is proportional to the multivariate variance for discrete characters (Foote and Miller, 2007). All characters were unordered and equally weighted. Phenetic distances between taxa ($S_{ij}$) were calculated using Gower’s coefficient (Gower, 1971), which rescales distances by the dividing by the number of comparable characters:

$$S_{ij} = \frac{\sum_{k=1}^{n} S_{ijk}}{\sum_{k=1}^{n} \delta_{ijk}}$$

where $\delta_{ijk}$ is equal to one if a character $k$ can be coded for species $i$ and $j$ and otherwise equal to zero (Lloyd, 2016). Temporal variation in morphospace occupation was assessed by assigning taxa to period-level bins and calculating disparity for each interval. Uncertainty in disparity estimates was evaluated using 1,000 bootstrap replicates.

To visually inspect morphospace distances between taxa in the complete dataset, a principal coordinate analysis (PCO) was conducted on the distance matrix. A phylomorphospace of the MCC tree was projected on species PCO scores distributed along the first two PCO axes, with ancestral state values inferred using maximum
likelihood (Revell, 2012) (Fig. 5.6). The first two PCO axes comprise 34.1% of the variance. Lower PCO 1 scores are associated with higher filtration fan densities, whereas higher scores are associated with lower filtration fan densities (Spearman’s $Rho = -0.772$, $P < 0.001$). Fan density reflects the presence of pinnules, number of distal arms, and arm type (e.g., uniserial/biserial). PCO 2 is inversely proportional to calyx complexity, where calyx complexity is defined as the number of primary calyx plates in the cup. Taxa with fewer calyx plates have higher PCO 2 scores (Spearman’s $Rho = -0.713$, $P < 0.001$). The spatial distribution of taxonomic clusters in principal coordinate space (Fig. 5.6) closely corresponds with previously identified grades of body plan organization in eu cladids (Kammer and Ausich, 1992, 1993, 1996; Webster and Maples, 2006; Wright, 2015).
References


Erwin, D.H., 2007, Disparity: morphological pattern and developmental context: 
     Palaeontology, v. 50, p. 57-73.
Foote, M. 1992, Paleozoic record of morphological diversity in blastozoan echinoderms: 
Foote, M., 1994, Morphological disparity in Ordovician–Devonian crinoids and the early 
Foote, M., 1996, Ecological controls on the evolutionary recovery of post-Paleozoic 
Foote, M., 1997, Estimating taxonomic durations and preservation probability: 
     Paleobiology, v. 23, p. 278–300.
Foote, M., 1999, Morphological diversity in the evolutionary radiation of Paleozoic and 
Foote, M., 2000, Origination and extinction components of taxonomic diversity: general 
Foote, M., and Raup, D.M., 1996, Fossil preservation and the stratigraphic ranges of taxa: 
     Paleobiology, v. 22, p. 121–140.


Simões, M., Breitkreuz, L., Alvarado, M., Baca, S., Cooper, J.C., Heins, L., Herzog, K. 
Trends in ecology & evolution, v. 31, p.27-34.


Slater, G.J., 2013, Phylogenetic evidence for a shift in the mode of mammalian body size 
evolution at the Cretaceous-Palaeogene boundary: Methods in Ecology and 
Evolution, v. 4, p. 734–744.

Slater, G.J., 2015, Not so early bursts and the dynamic nature of morphological 
3595-3596.

Slater, G.J., 2015, Iterative adaptive radiations of fossil canids show no evidence for 
diversity-dependent trait evolution: Proceedings of the National Academy of 

Slater, G.J., and Harmon, L.J., 2013, Unifying fossils and phylogenies for comparative 
analyses of diversification and trait evolution: Methods in Ecology and Evolution, 
v. 4, p. 699–702.

Slater, G.J., Price, S.A., Santini, F. and Alfaro, M.E., 2010, Diversity versus disparity and 
the radiation of modern cetaceans. Proceedings of the Royal Society of London B: 
Biological Sciences, v. 277, p. 3097-3104.


Webster, G.D., 2013, Bibliography and index of Paleozoic crinoids, coronates, and hemistreptocrinoids, 1758–2012: [http://crinoids.azurewebsites.net/]


Wright, D.F., 2015, Fossils, homology, and “Phylogenetic Paleo-ontogeny”: a reassessment of primary posterior plate homologies among fossil and living


**Figure 5.1 Macroevolutionary models of trait evolution.** Commonly used quantitative models of trait evolution among lineages are depicted as traitgrams. Models differ both conceptually and mathematically, especially how trait variation is expected to accumulate over time. Each represents a different ‘mode’ of evolution (Hunt and Carrano, 2010). Comparative data can be fitted to alternative models using likelihood or Bayesian frameworks, and parameter estimates can be used to infer evolutionary tempo and mode (but see Hunt, 2012). All models shown expect a degree of phylogenetic autocorrelation among species except “white noise”, which is equivalent to Brownian motion on a star phylogeny. Equations describing the models shown are described in Hansen (1997), Butler and King (2004), Felsenstein (2004), Harmon et al. (2010), and Paradis (2012).
Fig. 5.1
Fig. 5.2 Rates of phenotypic evolution in eucladid crinoids during the Paleozoic. The upper figure is the Maximum Clade Credibility tree from the Bayesian phylogenetic analysis. Major clades are identified at nodes. Median rates of morphologic evolution are shown along branches. Red branches indicate elevated rates and black branches indicate lower rates. Node bars are 95% highest probability densities for divergences. The lower figure are results from the maximum-likelihood analysis over a random sample of 100 time-calibrated trees from the Bayesian posterior distribution. Colored circles are mean rates and open circles represent medians. Red circles indicate intervals with >55% of sampled phylogenies were characterized by statistically high rates, whereas blue circles represent intervals where >55% of sampled phylogenies had statistically low rates (See Materials and Methods). Error bars represent 95% confidence intervals.
Fig. 5.2
Figure 5.3 Disparity and diversity profiles for Paleozoic eucladid crinoids. (Upper) Squares indicate the average pairwise distance among species placed in period-level bins. Note the Ordovician point is offset because eucladids originated during the Late Ordovician. Errors bars are 1 standard error based on bootstrap resampling. Although based on different taxon sampling strategies, discrete characters, and homologies, the major features and overall trajectory of this curve are strikingly similar to previous disparity profiles generated for Paleozoic eucladids (Foote, 1995 [fig. 15], 1999 [fig. 39]). (Middle) Circles represent taxonomic diversity, calculated as the number of genera per time bin using taxonomic first and last appearances recorded in Webster (2013). Errors bars are 1 standard error based on 1,000 bootstrap replicates. (Lower) Median diversity of taxa sampled for phylogenetic analysis calculated across 500 randomly sampled time-calibrated trees from the posterior distribution. Uncertainty around the median curve is indicated by the shaded region bounded by two-tailed 95% upper and lower quantiles.
Fig. 5.3
Figure 5.4 Time-varying diversification and sampling parameters estimated from phylogenetic analysis and stratigraphic ranges of genera. Net diversification (A), relative extinction (B), and sampling rates (C) from the Bayesian posterior distribution obtained from phylogenetic analysis. Points indicate median values for all parameter estimates in the posterior distribution. Error bars reflect 95% confidence intervals. The circles (D) represent net taxonomic diversification calculated at the genus-level, whereas the X’s indicate per-interval rates of turnover among genera (see Materials and Methods).
Fig. 5.4
Figure 5.5 Rates of morphologic evolution among eucladid subclades. Rates of morphologic evolution among the cyathoform (left) and cladoform (right) subclades of eucladid crinoids. Rates were inferred using the maximum-likelihood method over a random sample of 100 time-calibrated trees from the posterior distribution. Colored circles are mean rates and open circles represent medians. Error bars represent 95% confidence intervals.
Fig. 5.5
Figure 5.6 Identification of adaptive zones based on principal coordinate analysis of the morphologic character matrix. Adaptive zones are identified based on the clustering of taxa in morphospace. Zones were identified by rank correlation of PCO axes and morphologic traits (see Materials and Methods) and correspond with previously identified grades of body plan organization in eucladids (Kammer and Ausich, 1992, 1993, 1996; Webster and Maples, 2006; Wright, 2015).
Fig. 5.6
Figure 5.7 Phylomorphospace and adaptive zone occupation throughout the history of Paleozoic radiation. Results of principal coordinate analysis conducted on the entire matrix with taxa joined according to phylogenetic relationships implied by the MCC tree. The time-series shows morphologic disparity within eucladids through time and among clades. Taxa occurring within a timeslice are indicated by filled circles, whereas taxa not occurring within a timeslice are removed. Cyathoform taxa are distributed on the right hand side of PCO1, whereas taxa within cladoform subzones are in the center and left. See Figure 5.6 and the Materials and Methods section for delimitation and interpretation of eucladid adaptive zones.
**Figure 5.8 The relationship between taxonomic and morphologic diversification in Paleozoic eucladids.** Evolutionary radiation in Paleozone eucladid crinoids shown in a diversity-disparity plot. Taxonomic data were transformed to a log scale, generating a linear expectation in taxonomic diversification. Disparity and taxonomic diversity were range standardized using $\frac{(x_i - \min[x])}{(\max[x] - \min[x])}$. If data fall above the red line, disparification is outpacing diversification. If data instead fall below the red line, diversification is outpacing the rate at which morphologic innovation is generated. Data falling on the red line imply concordance between diversity and disparity. See Jablonski (in press) for additional information on types of evolutionary radiations in diversity-disparity space. Error bars are not shown (see Figure 5.9), but the Silurian and Devonian points are significantly above the 1:1 line and Pennsylvanian point falls significantly below it. Ord = Ordovician, Sil = Silurian, Dev = Devonian, Miss = Mississippian (early Carboniferous), Penn = Pennsylvanian (late Carboniferous), and Perm = Permian.
Fig. 5.8
Figure 5.9 Additional plots depicting the radiation of eucladids in diversity-disparity space. These plots are included to show uncertainty in taxonomic diversity and morphologic disparity plotted in diversity-disparity space. Error bars are 1 standard error from 1,000 bootstrap replicates. Unlike Figure 5.9, data were not range standardized. Note that taxonomic diversity is plotted on a log scale in the upper figure, but not in the lower figure.
Fig. 5.9
**Figure 5.10 Maximum Clade Credibility tree from Bayesian analysis of 81 Paleozoic euclidid crinoid species.** Node support is indicated by posterior probabilities. Basal nodes are well supported, but many more nested nodes are not. However, cyathoform and cladoform clades (see main text and Figure 5.3) are supported with PP = 1.
Fig. 5.10
Chapter 6: Crinoids from the Bobcaygeon and Verulam Formations (Upper Ordovician) near Brechin, Ontario: new taxa and emended descriptions

Abstract.— A survey of newly collected material from the Bobcaygeon and Verulam Formations reveals a large number of exceptionally preserved crinoid specimens. Focusing on taxa placed within the Cladida, this chapter contains taxonomic descriptions for eight species across five genera. The genus Konieckicrinus n. gen. n. sp. is proposed, comprised of two previously unknown species. In addition, descriptions for other species within the Brechin fauna are included, with comments on their taxonomic membership and recent changes in crinoid classification.

Introduction

The Ordovician is a key interval for understanding the evolutionary history and diversification of crinoids (Echinodermata, Crinoidea) because nearly all major clades first appear in Ordovician strata. After their initial diversification during the Early Ordovician, crinoids subsequently underwent a taxonomic and morphologic radiation coincident with the Great Ordovician Biodiversification Event (GOBE) and reached peak Ordovician diversity during the Sandbian. Following the GOBE, crinoid taxonomic
diversity dramatically declined and was decimated by the end-Ordovician mass extinction (Peters and Ausich, 2008).

The Upper Ordovician (lower Katian) Bobcaygeon and Verulam Formations near Brechin, Ontario are comprised of a highly diverse, well-preserved crinoid fauna. These “Brechin Fauna” crinoids are preserved alongside a rich Late Ordovician echinoderm community including representative ophiuroids, paracrinoids, cystoids, edrioasteroids, edrioblastoids, cyclocystoids, and homalozoans. This fauna provides an exceptional window into a taxonomically diverse Late Ordovician crinoid community from the interval between the Sandbian diversity peak and the end-Ordovician extinction. Although the sedimentology, stratigraphy and paleoecology of these Upper Ordovician strata have been studied in detail, the Brechin Fauna crinoids have not had a comprehensive taxonomic evaluation since Frank Springer’s (1911) classic monograph.

A survey of newly collected material from the Bobcaygeon and Verulam Formations reveals a large number of exceptionally preserved crinoid specimens with arms, stems, and attachment structures intact. Most importantly, this chapter describes two new, previously undescribed species and places them in a new genus. Many previously described species from this locality were based on incomplete material; thus, this new collection provides an opportunity to more fully describe morphologic details of known Ordovician crinoid taxa and to conduct a taxonomic re-evaluation.
Geographic and stratigraphic occurrences and geologic setting

Fossil material was collected from the Bobcaygeon and Verulam Formations (Upper Ordovician) exposed in the Lake Simcoe region near Brechin, Ontario (Fig. 6.1). Laurentia was located ~20° south of the equator during the Late Ordovician (Scotese and McKerrow, 1991) and sediments comprising both formations were deposited in warm water subtropical environments (Brett and Taylor, 1999, but see Brookfield, 1988 for an alternative interpretation). The Bobcaygeon Formation ranges in age from the Sandbian to Katian, whereas the Verulam is early Katian (Fig. 6.2). These strata consist of bioclastic wackestones, grainstones, and packstones interbedded with calcareous shales. The lithology of the Bobcaygeon Formation ranges from lime mudstone to grainstone dominant lithologies and are frequently interbedded with shale, suggesting deposition in lagoonal and shoaling settings to shallow shelf environments (Brookfield and Brett, 1988; Brett and Taylor, 1999). In contrast, limestones in the Verulam are somewhat thinner bedded and have greater proportion of interbedded shale, indicated deposition in a distal-shelf environment (Brett and Taylor, 1999). Both formations contain exceptionally preserved echinoderm faunas, including a diverse assemblage of crinoids. Although all major clades of Ordovician crinoids are represented in the Brechin fauna, cladids are the most abundant in the collections, especially cladids belonging to the Eucladida (Wright, in press) (Fig. 6.3).
Systematic paleontology

The classification system used here is from Wright et al. (in press). Morphologic terms follow Ubaghs (1978), Webster and Maples (2008), and Wright (2015). All measurements are in mm. References listed in the synonomies below can be found in Webster (2013). Specimen numbers refer to the reference numbers given by Joe Koniecki during collection and curation. Following publication of in prep manuscripts describing Brechin crinoids (Wright, in prep, Cole, in prep, Ausich et al., in prep), all fossils will be donated to the University of Michigan Museum of Paleontology and will be given museum new numbers when repositied. Although new species and genera are provided with taxonomic names, this dissertation chapter represents a nascent version of research currently in preparation for publication. All names, diagnoses, descriptions, and identifications are preliminary and should not be cited or used formally until results are published in a peer-reviewed journal.

Class Crinoidea Miller, 1821
Subclass Pentacrinoidea Jaekel, 1918
Infraclass Inadunata Wachsmuth and Springer, 1885
Inadunata incertae sedis: Family Metabolocrinidae Jaekel, 1902

Remarks.—The Metabolocrinidae are traditionally placed within the Cladida as defined by Moore and Laudon (1943). However, the phylogenetic position of the Metabolocrinidae
within the broader Pentacrinoidea clade is currently in question. Phylogenetic analysis of early to middle Paleozoic non-camerate taxa by Wright (in press) recovered *Metabolocrinus* as more closely related to the disparid clade than cladids, suggesting the metabolocrinids are in need of taxonomic revision. The Metabolocrinidae is therefore considered herein as Inadunata *incertae sedis*.

**Genus Konieckicrinus** new genus

*Type species.— Konieckicrinus brechinensis* new species.

**Diagnosis.—** Low bowl-shaped calyx, dicyclic, stellate plate sculpturing, second primibrachial axillary, pinnulate, arms branch isotomously on the second primibrachial, asymmetric endotomous to distal isotomous branching, brachials moderately cuneate, radianial in cup, located below and to the left of the C-ray radial, anal X above radianal, in contact the C-ray radial and supporting a median anal sac comprised of numerous tiny plates, column round, lumen round.

**Etymology.—** *Konieckicrinus* is named after Joseph Koniecki, who collected specimens of *Konieckicrinus* from quarries near Brechin.

**Remarks.—** *Konieckicrinus* is assigned to the Metabolocrinidae based on the presence of pinnules arms with endotomous branching. The presence of cuneate arms is
Konieckicrinus is most similar to the Ordovician genus Eopinnacrinus Brower and Veinus, 1982 which was placed in the Metabolocrinidae by Ausich (1998). Konieckicrinus differs from Eopinnacrinus in having asymmetric endotomous to isotomous branching above secundibrachials, stellate plate ornamentation, and an axillary on the second primibrachial.

Konieckicrinus brechinensis n. gen n. sp.

Figures 6.4-6.5

Holotype.—5097.2JK, paratype 5097.3JK.

Diagnosis.—Species of Konieckicrinus with asymmetric endotomous branching above secundibrachials.

Occurrence.—Bobcaygeon Formation, (Sandbian-Katian, Upper Ordovician), Ontario, Canada.

Description.—Calyx medium size, low bowl shape, base convex, stellate ornamentation on plates; infrabasals 5, visible from the side, basals 5, higher than wide, radials 5, plates larger than other calyx plates, subequal to slightly wider than high. Brachials moderately cuneate; pinnulate arms; first primibrachial wider than higher, axillary on the second primibrachial, triangular, branching with asymmetric
endotomy on secundibrachial 4-8, distal branches endotomous, with subequal rami arising from each axillary, three to six distal arms in each ray.

Radial beneath and to the left of the C ray radial plate, approximate size of basals; anal X above radianal, in contact with C ray radial, supporting a median column of anal sac plates.

Column circular, lumen round.

Etymology.—Named for the town of Brechin, Ontario, which is located near where the specimens were collected.

*Konieckicrinus* *josephi* n. gen n. sp.

Figures 6.6-6.8

*Holotype.*—5097.7JK, paratypes 5097.1JK, 5097.6JK.

*Diagnosis.*—Species of *Konieckicrinus* with distal isotomous branching above secundibrachials.

*Occurrence.*—Bobcaygeon Formation, (Sandbian-Katian, Upper Ordovician), Ontario, Canada.
Description.—Calyx small to medium size, low to moderate bowl shape, base convex, stellate ornamentation on plates; infrabasals 5, visible from the side, wider than high; basals 5, higher than wide, radials 5, larger than other calyx plates, wider than high.

Brachials moderately cuneate; pinnulate arms; first branching on the second primibrachial, branching isotonously above secundibrachials, typically at or above secundibrachial 8, distal branches endotomous to isotonous, with subequal rami arising from each axillary, three to six distal arms in each ray.

Radianal beneath and to the left of the C ray radial plate, approximate size of basals, anal X above radianal, in contact with C ray radial and CD basal, supporting a median column of anal sac plates, anal sac plates with stellate ornamentation.

Column circular, lumen round, attachment structure unknown, stem length is at least more twice that of crown.

Etymology.—Named for the town of Brechin, Ontario, which is located near where the specimens were collected.

Parvclass Cladida Moore and Laudon, 1943
Superorder Porocrinoidea, Wright, in press
Order Porocrinida Miller and Gurley, 1894
Genus *Illemocrinus* Eckert, 1987

Type species.—*Illemocrinus amphius* Eckert, 1987; by monotypy.
Other species.—Monospecific.

*Illemocrinus amphius* Eckert, 1987

Fig. 6.12


1993 *Illemocrinus amphius*; Webster, p. 72.

1988 *Illemocrinus amphius*; Ausich, p. 34.

Ocurrence.—Late Ordovician (Katian), Bobcaygeon Formation; Ontario, Canada.

Description.—Calyx small, medium bowl to globe shape; slightly higher than wide, infrabasals small, pentagonal; basal large, much higher than wide, with 5 to 6 ridges radiating from the center; radials 5, curved inward, slightly wider than high.

Radianal positioned below and to the left of the C ray radial, quadrangular; anal X above and to the right of the radianal, positioned in between the C and D ray radials, slightly larger than the radianal, supporting three additional anal plates above; anal sac massive, high, approximately twice the length of the calyx, comprised of stacked plates, becoming more irregular near the summit; anal sac plates with stellate ornamentation.
Brachials uniserial, wider than high; radial facets angustary, sloping down and inward; arms branch isotomously on the second primibrachial, higher branching isotomous up to at least four bifurcations.

Column pentagonal.

*Materials.*—5140.1JK.

Family Porocrinidae Miller and Gurley, 1894

Genus *Carabocrinus*

*Type species.*—*Carabocrinus radiatus* Billings, 1857.

*Other species.*—*Carabocrinus boltoni* Ausich and Copper, 2010; *C. crateriformis* (Hall, 1866); *C. conoideus* Sardeson, 1925; *C. dicyclicus* (Sardeson, 1899); *C. esthonus* Jaekel, 1918; *C. geometricus* Hudson, 1905; *C. granulosus* Evans, 1926; *C. huronensis* Foerste, 1924; *C. magnificus* Sardeson, 1939; *C. micropunctatus* Brower and Veinus, 1974; *C. oogyi* Kolata, 1975; *C. ovalis* Miller and Gurley, 1894; *C. stellifer* Brower and Veinus, 1974; *C. treadwelli* Sinclair, 1945; *C. vancortlandti*.

*Carabocrinus radiatus* Billings, 1857

Fig. 6.9

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1859 *Carabocrinus radiatus*; Billings p. 31, pl. 2, figs. 3a-3e.

1868 *Carabocrinus radiatus*; Shumard, p. 357.

1868 *Carabocrinus radiatus*; Bigsby, p. 18.

1889 *Carabocrinus radiatus* S.A. Miller, p. 182.

1910 *Carabocrinus radiatus*; Grabau and Shimer, p. 504, fig. 1817.

1912 *Carabocrinus cf. radiatus*; Ruedemann, p. 86, pl., 3, fig. 6.

1915 *Carabocrinus radiatus*; Basser, p. 183.

1915 *Carabocrinus cf. radiatus*; Basser, p. 183.

1938 *Carabocrinus radiatus*; Bassler, p. 60.

1943 *Carabocrinus radiatus*; Bassler and Moodey, p. 356.

1943 *Carabocrinus radiatus*; Moore and Laudon, p. 153, pl., 53, fig. 5.

1946, *Carabocrinus radiatus*; Wilson, p. 38, pl., 5, fig. 5.

1973 *Carabocrinus radiatus*; Webster, p. 78.


**Occurrence.**—Late Ordovician (Katian), New York, Iowa; Bobcaygeon Formation; Ontario, Canada.

**Description.**—Calyx low, rounded base; relatively wide; bearing multiple stellate ridges; exothecal respiratory canals; infrabasals 5, visible in side view, slightly wider than high,
pentagonal; basals large, hexagonal to septagonal, slightly higher than wide; radials 5, wider than high.

Radial anal split into infer- and superradianals, between CD and BC interray basals, higher than wide; anal X located above and to the left of the superradianal.

Uniserial brachials; narrow, angustary radial facets; isotomous branching on the second primibrachial; higher branching isotomous to somewhat heterotomous.

Proximal column circular.

*Materials.*—5080.2bJK and 5080.2cJK.

*Carabocrinus vancortlandti* Billings, 1859

Figs. 6.10

1859 *Carabocrinus vancortlandti* Billings, p. 52, pl, 2, fig. 4.
1868 *Carabocrinus vancortlandti*; Shumard, p. 357.
1868 *Carabocrinus vancortlandti*; Bigsby, p. 18.
1889 *Carabocrinus vancortlandti*; Miller, S.A. p. 231.
1900 *Carabocrinus vancortlandti*; Weller, p. 28, fig. 9.
1943 *Carabocrinus vancortlandti*; Bassler and Mooeey, p. 356.
1943 *Carabocrinus vancortlandti*; Moore and Laudon, p. 153, pl., 53, fig. 6.
1973 *Carabocrinus vancortlandti* Webster, p. 78.
1996 *Carabocrinus vancortlandti* Brower, p. 617, figs. 4-5.

**Occurrence.**—Middle to Late Ordovician (Darriwilian-Katian), Iowa, Kentucky, United States; Ontario, Canada.

**Description.**— Calyx high, rounded base and side; oval to egg shaped; bearing multiple, well-defined stellate riches; exothecal respiratory canals; infrabasals 5, visible in side view, slightly wider than high, pentagonal; basals large, hexagonal to septagonal, slightly higher than wide; radials 5, wider than high.

Radial anal split into infer- and superradians, between CD and BC interray basals, both plates higher than wide; anal X located above and to the left of the superradianal.

Uniserial brachials; narrow facets, angustary; isotomous branching on the second primibrachial; higher branching isotomous, higher axillaries on different secundibrachials within each ray.

Proximal column circular, at least three time the length of the crown.

**Materials.**—5143JK.

Magnorder Eucladida Wright, in press

Superorder Cyathoformes Wright et al., in press

*Cyathoformes incertae sedis*: “Dendrocrinida” Bather, 1899

Family Dendrocrinidae Wachsmuth and Springer, 1886
Genus *Grenprisia* Moore, 1962

*Type species.*—*Grenprisia billingsi* Moore, 1962.

*Other species.*—*G. springeri* Moore, 1962.

*Grenprisia billingsi* (Springer, 1911)

1911 *Ottawacrinus billingsi* Springer; p. 40, pl. 4, figs. 1-4.
1915 *Ottawacrinus billingsi*; Bassler, p. 926.
1943 *Ottawacrinus billingsi*; Bassler and Moodey, p. 577.
1944 *Ottawacrinus billingsi*; Moore and Laudon, p. 158, pl. 53, fig. 23.
1962 *Grenprisia billingsi*; Moore, p. 38.
1973 *Grenprisia billingsi*; Webster, p. 143.
1978 *Grenprisia billingsi*; Brower and Veinus, p. 443, pl. 13, figs. 1-4.
1978 *Grenprisia billingsi*; More and Lane, p. T612, figs. 397, nos. 2a-2g.
1986, *Grenprisia billingsi*; Webster, p. 162.

*Occurrence.*—Late Ordovician (Katian), Hull Limestone, Bobcaygeon Formation; Ontario, Canada.

*Materials.*—5110.2JK.
Grenprisia springeri (Springer, 1911)

Fig. 6.11

1911 *Ottawacrinus typus* Springer 1911 (non Billings, 1887), p. 37, pl. 4, figs. 5-7.

1962 *Grenprisia springeri*; Moore, p. 38.

1973 *Grenprisia springeri*; Webster, p. 143.

1978 *Grenprisia springeri*; Moore and Lane, p. T612, fig. 397, no. 2h.

1986 *Grenprisia springeri*; Webster, p. 162.

**Occurrence.**—Late Ordovician (Katian), Hull Limestone, Bobcaygeon Formation; Ontario, Canada.

**Description.**—Calyx medium to small in size, high bowl shape, flat base; infrabasals large, visible from the side, subequal; basals large, equal in size or larger than radials; radial plates wider than high.

Radialanal large, directly above posterior basal plate, supporting an anal X and right tube plate above leading to an anal sac; cylindrical, large anal sac, comprised of small plates with stellate ornamentation.

Arms uniserial; heterotomous, branching isotonously on primibrachial 3, multiple bifurcations above secundibrachials.

Pentemeric stem, transversely pentagonal.
Materials.—5110.11JK.

Remarks.—*Grenprisia billingsi* is distinguished from *G. springeri* by its much larger size and heterotomous arms with secondary ramules that only branch on one side, whereas *G. springeri* is much smaller and typically has isotomous branching arms with one or two bifurcations (Springer, 1911).

Superorder Flexibilia Zittel, 1895

Remarks.—The Flexibilia have traditionally been considered a subclass of crinoids (e.g., Moore and Teichert, 1978). However, it has been hypothesized since Springer (1911, 1920) that flexible crinoids descended from ancestors that were placed within the Cladida, rendering the cladids paraphyletic. Simms and Sevastopulo (1993) recommended the Flexibilia be placed within the Cladida to eschew paraphyly in the classification of crinoid higher taxa. Wright et al.’s (in press) revised classification of the Crinoidea follows Simms and Sevastopulo (1993) and placed the Flexibilia as a superorder within the Cladida.
Remarks.—The Cupulocrinidae was originally erected by Moore and Laudon (1943) as a monogeneric family of Ordovician crinoids from North America. However, *Morenacrinus* Ausich, Gil Cid, and Alonso, 2002 from the Darriwilian of Spain and *Stewbrecrinus* Jell, 1999 from the Devonian of Australia have since been placed within the family. Building on the work of Springer, 1920, a recent phylogenetic analysis of Wright (in press) found evidence to support *Cupulocrinus heterocostalis* as potentially ancestral to flexible crinoids. Wright et al. (in press) presented a phylogeny-based revision to crinoid classification and suggested *Cupulocrinus* be included within the definition of the flexible clade. Thus, the monophyly of the family is in question. However, a comprehensive revision is beyond the scope of this chapter.

Genus *Cupulocrinus* d’Orbigny, 1849

*Type species.*—*Cupulocrinus heterocostalis* (Hall, 1847).

*Other species.*—*Cupulocrinus angustatus* (Meek and Worthen, 1870); *C. australogracilis* Jell, 1999; *C. canaliculatus* Brower and Veinus, 1978; *C. crossmani* Brower, 1992; *C. heterobrachialis* Rambsbottom, 1961; *C. humilis* (Billings, 1857); *C. jewetti* (Billings, 1859); *C. kentuckiensis* Springer, 1911; *C. latibrachiatus* (Billings, 1857); *C. leversoni* Kolata, 1986; *C. minimus* Springer, 1911; *C. minimus* Springer 1911; *C. molanderi*
Kolata, 1975; *C. plattesvillensis* Kolata, 1975; *C. sepulchrum* Ramsbottom, 1961; *C. tuberculatus* d’Orbigny, 1847.

*Cupulocrinus humilis* (Billings, 1857)

Fig. 6.13

1857 *Dendrocrinus humilis* Billings, 1857, p. 270.

1859 *Dendrocrinus humilis*; Billings, p. 39.pl. 3, fig. 4.

1868 *Dendrocrinus humilis*; Shumard, p. 365.

1868 *Dendrocrinus humilis* Bigsby, p. 19.

1889 *Dendrocrinus humilis* Miller, 1889, p. 238.

1911 *Cupulocrinus humilis*; Springer, 1911, p. 28, pl. 1, figs. 8-9.

1915 *Cupulocrinus humilis*; Bassler, p. 315.

1943 *Cupulocrinus humilis*; Bassler and Moodey, p. 387.

1943 *Cupulocrinus humilis*; Moore and Laudon, p. 155, pl., 53, figs. 7, 25.

1953 *Cupulocrinus humilis*; Ubaghs, p. 751, figs. 14, no. b.

1973 *Cupulocrinus humilis*; Webster, p. 92.

1975 *Cupulocrinus humilis*; Kolata, p. 38, pl. 6, fig. 7.

1978 *Cupulocrinus humilis*; Ubaghs, p. T125, fig. 94, no. 2.


1986 *Cupulocrinus humilis*; Webster, p. 111.

1988 *Cupulocrinus humilis*; Webster, p. 63.

2005 *Cupulocrinus humilis* Sloan, p. 153, fig. 4, no. 6.
Ocurrence.—Late Ordovician (Katian), Kentucky, New York, Minnesota, United States; Ontario, Canada.

Description.—Calyx conical, flat based, much higher than wide, smooth; infrabasals 5, pentagonal, higher than wide; basals large, hexagonal, comprising >50% of calyx height, radials subequal in height:width, closely spaced, abutting one another.

Radianal large, approximate in size to radials, hexagonal, located directly beneath the C-ray radial plate, in contact with CD and BC basal plates; anal X similar in size to other calyx plates, higher than wide, above and to the left of radianal, situated between the C and D radials, supporting sac plates above; anal sac tube-like, erect, consisting of stacked, rounded plates, distally tapering.

Brachials uniseral, much wider than high, narrowing distally; radial facets wide, extending across the full width of the radial facets; weakly developed “petelloid” process, number of primibrachials variable, branching isotomously on primibrachials 4-12; higher bifurcations isotomous to heterotomous;

Column circular; proximal portion wider than the rest of the stem; large nudinodals, regularly spaced.

Materials.—5115JK and 5123.2JK.
Cupulocrinus jewetti (Billings, 1859)

Fig. 6.14

1859 Dendrocrinus jewetti Billings, E., p. 43, fig. 13.
1868 Dendrocrinus jewetti; Shumard, p. 356.
1868 Dendrocrinus jewetti; Bigsby, p. 19.
1883 Dendrocrinus jewetti; Billings W.R., p. 51.
1889 Dendrocrinus jewetti; Miller, p. 238, fig. 283.
1911 Cupulocrinus jewetti; Springer, p. 28, pl. 1, figs. 10-12, pl. 3, figs. 5-7c.
1915 Cupulocrinus jewetti; Bassler, p. 315.
1915 Dendrocrinus jewetti, Bassler, p. 315.
1920 Cupulocrinus jewetti; Springer, p. 88, pl. 75, figs. 2-4.
1943 Cupulocrinus jewetti; Bassler and Moodey, p. 387.
1943 Cupulocrinus jewetti; Moore and Laudon, p. 155, pl 53, fig. 12.
1970 Cupulocrinus jewetti; Norford et al., p. 606, pl 4, fig. 12.
1970 Cupulocrinus jewetti; Bolton, p. 63, pl. 13, fig. 12.
1972 Cupulocrinus jewetti; Bolton and Copeland, p. 54, pl. A, fig. 22.
1977 Cupulocrinus jewetti; Webster, p. 62.
1978 Cupulocrinus jewetti; Frest and Strimple, p. 688, fig. 7, no. A.
1978 Cupulocrinus jewetti; Brower and Veinus, p. 430, pl. 14, figs. 1-4, pl. 15, figs. 4, 7.
1978 Cupulocrinus jewetti; Moore, p. T627, fig. 409, no. 2a-2b.

1986 *Cupulocrinus jewetti*; Kolata, p. 714, fig. 2, no. 1.

1986 *Cupulocrinus jewetti*; Webster, p. 111.

1988 *Cupulocrinus jewetti*; Webster, p. 63.

1993 *Cupulocrinus jewetti*; Webster, p. 45.

1999 *Cupulocrinus jewetti*; Brett and Taylor, p. 69, fig. 80, no. e, Fig. 83.

**Occurrence.**—Late Ordovician (Katian), Kentucky, Wisconsin, Minnesota, Illinois, United States; Ontario, Canada.

**Description.**—Calyx conical to medium bowl shape, flat based, widest at the summit, smooth; infrabasals 5, pentagonal, higher than wide; basals large, hexagonal, comprising >50% of calyx height, radials subequal in height:width, closely spaced, abutting one another.

Radialanal large, approximate in size to radials, hexagonal, located directly beneath the C-ray radial plate, in contact with CD and BC basal plates; Anal X similar approximate size of radials, subequal, above and to the left of radialanal, situated between the C and D radials, supporting sac plates above; anal sac tube-like, erect, consisting of stacked, rounded plates, distally tapering, with a median keel.

Brachials uniseral, much wider than high, narrowing distally; radial facets wide, extending across the full width of the radial facets; “petelloid” process, number of
primibrachials roughly constant, three in posterior rays, branching isotonously on
primibrachials 4-12; higher bifurcations isotonous to heterotomous.

Column circular; proximal portion does not widen near calyx.

*Materials.*—5028.1.
References


Moore, R.C., and Teichert, C., eds., 1978, Treatise on Invertebrate Paleontology, Part T, Echinodermata 2: Geological Society of America and University of Kansas Press, Lawrence, Kansas, 1027 p.


Figure 6.1 Locality map of the Lake Simcoe region in Ontario.
Fig. 6.1
Figure 6.2 Stratigraphy of the Simcoe Group highlighting the position of the Bobcaygeon and Verulam Formations. (Modified from Sproat et al., 2015).
Fig. 6.2
Figure 6.3 Abundance distribution of specimens represented in the Brechin collections. Number of specimens for in the collections for higher taxa. Note that cladids are far more abundant than camerates or disparids and most cladids belong to the Eucladida rather than the Flexibilia or Hybocrinida (see Wright, in press).
Fig. 6.3
Figure 6.4 *Konieckicrinus brechinensis* n. gen. n. sp., specimen 5097.2. Bobcaygeon Fm., Carden Quarry.
Figure 6.5 *Konieckicrinus brechinensis* n. gen. n. sp., specimen 5097.3. Bobcaygeon Fm., LaFarge Quarry.
Fig. 6.5
Figure 6.6 *Konieckicrinus josephi* n. gen. n. sp., specimen 5097.7JK. Bobcaygeon Fm., Carden Quarry.
Figure 6.7 *Konieckicrinus josephi* n. gen. n. sp., specimen 5097.1JK. Bobcageon Fm., LaFarge Quarry.
Fig. 6.7
Figure 6.8 *Konieckicrinus josephi* n. gen. n. sp., specimen 5097.6. Bobcaygeon Fm., Carden Quarry.
Figure 6.9 *Carabocrinus radiatus* Billings, 1857. Specimens 5080.2b (left) and 5080.2c (right), Bobcaygeon Fm., Carden Quarry.
Fig. 6.9
Figure 6.10 *Carabocrinus vancortlandti* Billings, 1859. Specimen 5413JK, preserved on a slab with the camerates *Cleiocrinus* and *Periglyptocrinus*; Bobcaygeon Fm., LaFarge Quarry.
Fig. 6.10
Figure 6.11 *Grenprisia springeri* Moore 1962. Specimen 5110.11JK, Bobcaygeon Fm.
Figure 6.12 *Illemocrinus amphiatius* Eckert, 1987. Specimens 5140.1JK (left) and 5140JK (right), Bobcaygeon Fm.
Fig. 6.12
Figure 6.13 *Cupulocrinus humilis* (Billings, 1857). Specimen 5115 (left), Bobcaygeon Fm.; 5123.2 (right), Verulam Fm.
Fig. 6.13
Figure 6.14 *Cupulocrinus jewetti* (Billings, 1859). Specimen 5028.1, Bobcaygeon Fm., Carden Quarry. Note regenerating arms.
References


Bapst, D.W., and Hopkins, M.J., in press, Comparing cal3 and other a posteriori time-scaling approaches in a case study with the Pterocephaliid trilobites: Paleobiology.


347


354


359


Hall, B. K., 2003, Descent with modification: the unity underlying homology and homoplasy as seen through an analysis of development and evolution: Biology Reviews, v. 78, p. 409-433.


Hunt, G., 2008, Gradual or pulsed evolution: when should punctuational explanations be preferred?: Paleobiology, v. 34, p.360–377.


Jablonski, in press, Macroevolutionary theory, *in* Scheiner, S.M., and Mindell, D.P.,

Jaekel, O., 1894, Über die Morphogenie und Phylogenic der Crinoiden: Sitzungsberichten der

Jaekel, O., 1902, Über verschiedene Wege phylogenetischer Entwicklung: 5th Verhandlungen

Jaekel, O., 1906, Der oberste Lenneschiefer zwischen Letmathe und Iserlohn *in* Schmidt, W.E.,
Der oberste Lenneschiefer zwischen Letmathe und Iserlohn: Zeitschrift der Deutschen

Jaekel, O., 1918, Phylogenie und System der Pelmatozoen: Paläontologische Zeitschrift,
v. 3, p. 1–128.

Kammer, T.W., Aerosol filtration theory applied to Mississippian deltaic crinoids:

Kammer, T.W., 2001, Phenotypic bradytely in the *Costalocrinus-Barycrinus* lineage of

Kammer, T.W. 2008, Paedomorphosis as an adaptive response in pinnulate cladid
crinoids from the Burlington Limestone (Mississippian, Osagean) of the
Echinoderm Paleobiology, University of Indiana Press, Bloomington.

Kammer, T.W., and Ausich, W.I., 1992, Advanced cladid crinoids from the Middle
Mississippian of the east-central United States. primitive-grade calyces: *Journal of

366


Lane, N.G., 1970, Lower and Middle Ordovician crinoids from west-central Utah: Brigham Young University Geology Studies, v. 17, p. 3–17.


Matsumoto, H., 1929, Outline of a classification of Echinodermata: Science Reports of the Tohoku Imperial University, Sendai, Japan, Second Series (Geology): v. 8, p. 27–33.


Miller, S.A., 1883, The American Palaeozoic fossils: a catalogue of the genera and species, with names of authors, dates, places of publication, groups of books in which found, and the etymology and significance of the words, and an introduction devoted to the stratigraphical geology of the Palaeozoic rocks, 2nd edition, Echinodermata, Cincinnati, Ohio, p. 247-334.


Moore, R.C., and Teichert, C., eds., 1978, Treatise on Invertebrate Paleontology, Part T, Echinodermata 2: Geological Society of America and University of Kansas Press, Lawrence, Kansas, 1027 p.


Phillips, J., 1841, Figures and descriptions of the Palaeozoic fossils of Cornwall, Devon, and West Somerset; observed in the course of the ordinance geological survey of that district: London, Longmans, Brown, Green, and Longmans, 232 p.


Rambaut, A., and Drummond, A.J., 2015, TreeAnnotator v2 2.1: MCMC ouput analysis.


Schultze, L., 1867, Monographie der Echinodermen des Eifler Kalkes: Denkschriften der
Kaiserlich Akademie der Wissenschaften Mathematisch-Naturwissenschaftlichen


Sereno, P.C., 1999, Definitions in phylogenetic taxonomy: critique and rationale:


for suprageneric taxa and phylogenetic definitions: PhyloInformatics, v. 8, p. 1–
21.

Sevastopulo, G.D., and Lane, N.G., 1988, Ontogeny and phylogeny of disparid crinoids,
in Paul, C.R.C., and Smith, A.B., eds, Echinoderm phylogeny and evolutionary

Signor P.W., and Brett, C.E., 1984, The mid-Paleozoic precursor to the Mesozoic marine


383
Slater, G.J., 2013, Phylogenetic evidence for a shift in the mode of mammalian body size evolution at the Cretaceous-Palaeogene boundary: Methods in Ecology and Evolution, v. 4, p. 734–744.


Smith, A.B., 1990, Evolutionary diversification of the echinoderms during the Early

Smith, A.B., 1994, Systematics and the Fossil Record: Documenting Evolutionary

Smith, A.B., 2001, Large-scale heterogeneity of the fossil record: implications for
Phanerozoic biodiversity studies: Philosophical Transactions of the Royal

255-280.

Smith, A.B., 2008, Duterostomes in a twist: the origins of a radical new body plan:

Smith, A.B., and Jell, P.A., 1990, Cambrian edrioasteroids from Australia and the origin

Smith, A.B., and Zamora, S., 2013, Cambrian spiral-plated echinoderms from Gondwana
280:20131197, doi.org/10.1098/rspb.2013.1197

Smith, A.B., Lafay, B., and Christen, R., 1992, Comparative variation of morphological
and molecular evolution through geologic time: 28S ribosomal RNA versus
morphology in echinoids: Philosophical Transactions: Biological Sciences, v.

Snively, E., Russell, A.P. and Powell, G.L., 2004, Evolutionary morphology of the
coeurosaarian arctometatarsus: descriptive, morphometric and phylogenetic

Soul, L.C., and Friedman, M., 2015, Taxonomy and phylogeny can yield comparable results in comparative paleontological analyses: Systematic Biology, v. 64, p. 608–620.


Stadler, T., Kouyos, R., Wyl, V. von, Yerly, S., Böni, J., Bürgisser, P., Klimkait, T., Joos, B., Rieder, P., Xie, D., Günthard, H. F., Drummond, A. J., Bonhoeffer, S., the Swiss


von Baer, K. E., 1828, Uber Entwickelungsgeschichte der Thiere: Beobachtung und Reflektion, Bornträger.


Webster, G.D., 2013, Bibliography and index of Paleozoic crinoids, coronates, and hemistreptocrinoids, 1758–2012: [http://crinoids.azurewebsites.net/]


Wetherby, A.G., 1880, Remarks on the Trenton Limestone of Kentucky, with descriptions of new fossils from that formation and the Kaskaskia (Chester)


Wright, D.F., 2015, Testing the taxonomic structure of Paleozoic pan-cladid crinoids: a statistical approach using the fossilized birth-death process and Bayesian


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Appendix A: Character list for phylogenetic analysis in Chapter 5.

1. Calyx shape ratio (height /width): very high, >1.5 (0); high, 1.5-1.0 (1); intermediate 1.0-0.5 (3); low, 0.5-0.25 (3); very low, < 0.25 (4).
2. Calyx profile: straight sided, cone shape (0); rounded base with widest point at the summit of the calyx (1); rounded base with widest point below the summit of the cup (2).
3. Calyx shape in transverse section: round (0); subpentagonal (1).
4. Calyx radial plate thickness: thin, <25% height or width of plate (0); thick, >25% height or width of plate (1).
5. Calyx plate sculpturing: absent (0); present (1).
6. Type of calyx suturing: non-stellate ridges (0); stellate ridges (1); spinose (2); nodose (3); granulose (4).
7. Outline shape of calyx base: upright (0); broad and flat (1); steeply concave (2).
8. Basal invagination of calyx: absent (0); present (1).
9. Attitude of the infrabasal cirplet: all plates visible in side view (0); along base of calyx, neither entirely in a basal concavity nor visible in side view (1); not visible in side view (2).
10. Number of infrabasal plates: five (0); three (1); one (2).
11. Infrabasal plate dimensions: width > height (0); width ~ height (1); width < height (2).

12. Cross sectional shape of the infrabasal plates: straight upwards/flared (0); curved/downflared (1).

13. Attitude of the basal circlet: all plates visible in side view (0); along base of calyx, neither entirely in a basal concavity nor visible in side view (1); not visible in side view (2).

14. Basal plate dimensions: width > height (0); width ~ height (1); width < height (2).

15. Relative sizes of plates in the basal circlet: equal/subequal (0); unequal (1).

16. Cross sectional shape of the basal plates: straight (0); curved (1); bulbous/inflated (2).

17. Interruption in the radial circlet CD interray: absent (0); present (1).

18. Radial plate dimensions: width > height (0); width ~ height (1); width < height (2).

19. Attitude of the radial circlet: (0); along base of calyx, neither entirely in a basal concavity nor visible in side view (1).

20. Cross sectional shape of the radial plates: straight (0); curved (1); bulbous/inflated (2).

21. Largest plate in the calyx: below the radials circlet (0); in the radial circlet (1).

22. Compound/bi-radial: absent (0); present (1).

23. C-ray radial plate: similar size to other radial plates (0); smaller than other radial plates (1).

24. Radial facet width (*sensu* Webster and Maples 2008): angustary (0); peneplenary (1); plenary (2).
25. Contact type when radial facets extend across the radial plate (Webster 2007): plenary (0); explenary (1); inplenary (2).

26. Radial facet dimensions: width > height (0); width ~ height (1); width < height (2).

27. Adaxial notch on radial facets: absent (0); present (1).

28. Orientation of the radial facets: planate (0); declivate (1); sursumate (2).

29. Radial facet type (*sensu* Webster and Maples, 2008): unifascial (0); bifascial (1); multifascial ‘muscular’ (2); trifascial (3).

30. Transverse ridge on radial facet: absent (0); present (1).

31. Thick entoneural canal on facet: absent (0); present (1).

32. Ligament pit on facet: absent (0); present (1).

33. Crenulated surface proximal to aboral ligamentary fossae: absent (0); present (1).

34. Number of posterior plates partially or completely within the cup: three (0); ≤ three (1).

35. Radianal plate: absent (0); present (1).

36. Visibility of the radianal plate: visible on the exterior (0); cryptic (1).

37. Shape of the radianal plate (upper plate when subdivided): pentagonal (0); tetragonal (1); hexagonal (2).

38. Proximal position of the radianal plate: full width beneath the C-ray radial (0); to the left and below the C radial plate (1); within the radial circlet above the CD basal plate (2).

39. Circlet in most proximal position with the radianal plate: basals (0); infrabasals (1); radials (2).
40. Anal X: absent (0); present (1).

41. Shape of the anal X plate: pentagonal (0); tetragonal (1); hexagonal (2);

42. Position of the anal X plate within the calyx: entirely in the cup (0); partially in the
cup (1); entirely above the cup (2).

43. Position of the anal X plate relative to the plates below: above and to the left of the
radianal and in contact with the CD basal (0); above and to the left of the radianal
and in contact with the D radial but not the CD basal (1); directly above the
radianal and not in proximal contact with the CD basal or the D radial (2).

44. Plates right-lateral to the anal X: in contact with the C-ray radial (0); in contact with
other anal plates (1).

45. Right tube plate: absent (0); present (1).

46. Shape of the right tube plate: pentagonal (0); tetragonal (1); hexagonal (2).

47. Position of the right tube plate within the calyx: entirely in the cup (0); partially in the
cup (1); entirely above the cup (2).

48. Position of the right tube plate relative to the plates below: above and to the right of
the anal X and in contact with the radianal (0); directly above the anal X and not
in contact with the radianal (1); above and to the right of the anal X and not in
contact with the radianal (2).

49. Plates left-lateral to the right tube plate: anal X and additional anal plates (0); anal X
only (1); D-ray radial plate (2).

50. Anal sac: absent (0); present (1).
51. Height of the anal opening above the cup: ≤ half the height of the arms (0); > half the height of the arms and ≤ maximum arm height (1); > than maximum arm height (2).

52. Anus position relative to the crown: near the summit (0); below the summit (1).

53. Anal sac plating: vertical columns, regular plating (0); irregular plating (1).

54. Medial column supporting the anal sac: absent (0); present (1).

55. Anal sac plate sculpturing: absent (0); present (1).

56. Anal sac sculpturing pattern: radiating ridges (0); vertical grooves and ridges (1).

57. Anal sac plate cross section: flat (0); convex (1); spinose (2); plicated (3).

58. Shape of the anal sac: cylindrical (0); tapers distally (1).

59. Pore structures on the anal sac: absent (0); present (1).

60. Anal sac spines: absent (0); present (1).

61. Number of arm openings originating from the calyx: five (0); three (1); one (2).

62. Arrangement of spines along the anal sac summit: single spine (0); multiple spines (1); roof-forming (e.g., “umbrella” of spines).

63. Arm openings into the calyx: five (0); three (1); one (2).

64. Proximal free arm projection: outward and upward (0); directed vertically (1).

65. Fixed lower brachial plates: absent (0); present (1).

66. Primaxil branching on B-E rays: absent (0); present (1).

67. Branching in the A ray: same as B-E rays (0); different from B-E rays (1).

68. Highest position of an axillary on B-E ray primibrachials: IPr1 (0); IPr2 (1); ≥ IPr3 (2).
68. Bifurcation pattern on B-E ray primaxils: atomous (0); similar spacing (1); irregular spacing (2); plates fuse to form a mesh/fan shape (3).

69. Spacing between axillaries at and above the second brachitaxes in B-E rays: regular (0); irregular (1).

70. Secundaxil branching in the B-E rays: absent (0); present (1).

71. Branching above the secundaxil in B-E rays: absent (0); present (1).

72. Largest number of axillaries per ray: zero (0); one (1); two (2); ≥ 3 (3).

73. Outline pattern of bifurcation (Ubaghs, 1978, fig. 115): isotomous (0); heterotomous (# 2 and 3 in Ubaghs, 1978, fig 115) (1); endotomous (2); exotomous (3).

74. Pinnulation: absent (0); present (1).

75. Branching complexity of minor arm appendages on brachials distributed along the main ray axis: absent (0); ramulate (i.e., terminal appendages are separated by at least one brachial, branched or unbranched) (1); pinnulate (i.e., unbranched terminal appendages distributed along successive brachial plates) (2).

76. Mature (i.e., distal) brachial type: uniserial (0); biserial (1).

77. Transition from proximal uniserial to distal biseral brachials: absent (0); present (1).

78. Mature shape of uniserial brachials (sensu Webster 2007): rectilinear (0); weakly cuneate (1); moderately cuneate (2); strongly cuneate (3).

79. Distal biserial brachial shape (sensu Webster 2007): wedge (0); round (1); flat chisel (2).

80. Size of the primibrachials: smaller than radials (0); subequal to radials (1).
81. Number of axillaries in the A ray: same as other rays (0); first branching is higher than other rays (1).

82. Shape of the first primibrachial: tetragonal (0); pentagonal (1); triangular (2).

83. Dimensions of the first primibrachial: width > height (0); width ~ height (1); width < height (2).

84. Primaxil ornamentation: absent (0); present (1).

85. Maximum number of secundibrachials: zero (0); one (1); two (2); ≥ 3 (3).

86. Secundaxil spines: absent (0); present (1).

87. Syzygial sutures on brachials: absent (0); present (1).

88. Column: absent (0); present (1).

89. Proximal shape of the stalk: circular (0); pentagonal (1).

90. Lumen shape in proxistele columnals: circular (0); pentalobate (1); pentastellate (2).

91. Branching appendages on proximal stem: absent (0); present (1).

92. Stem appendages: absent (0); cirri (1); highly cirriferous (2).