Swiss Journal of Palaeontology (2018) 137:159–176
https://doi.org/10.1007/s13358-018-0147-z

REGULAR RESEARCH ARTICLE

Morphological paradox of disparid crinoids (Echinodermata): phylogenetic analysis of a Paleozoic clade

William I. Ausich[1]

Received: 19 January 2018 / Accepted: 6 March 2018 / Published online: 3 April 2018

Abstract
Phylogenetic relationships within the parvclass Disparida are evaluated using parsimony-based phylogenetic methods. The Disparida is a combination of forms with simplified morphologies and forms with highly specialized morphologies. The latter, e.g., Acolocrinidae, Calceocrinidae, Catillocrinidae, and Myelodactylidae, are consistently identified as clades, as are some simplified forms, such as the Allagecrinidae, Eustenocrinidae, and Tetragonocrinidae. The Iocrinidae is typically recovered as a paraphyletic grade between the outgroup the oldest disparid, *Alphacrinus*, and more tipward disparids. The primary aspects of disparid phylogeny that remain ambiguous using parsimony analysis are the Cincinnaticrinidae and Homocrinidae, each of which is broadly paraphyletic with taxa in basal and/or derived positions, the status of several monogeneric families, and the phylogenetic position of disparids too poorly known to include in phylogenetic analysis.

Keywords Crinoidea · Disparida · Phylogeny · Ordovician · Silurian

Introduction

The parvclass Disparida (sensu Wright et al. 2017) was traditionally understood as a monocyclic order within the Inadunata (sensu Moore and Teichert 1978) and is presently defined phylogenetically with the stem-based definition as "the most inclusive clade containing *Synbathocrinus conicus* Phillips (1836) but not *Dendrocrinus longidactylus* Hall (1852)" (Wright et al. 2017). This clade ranged from the Early Ordovician to the Middle Permian. Disparids as a whole are a fascinating group of Paleozoic crinoids that generally are highly simplified, yet certain clades are among the most morphologically specialized Paleozoic crinoids known, such as the bilaterally symmetrical Calceocrinidae that were recumbent on the sea floor with their arms along their column when in a closed, resting posture (Moore 1962a; Brower 1966; Ausich 1986a) or the Zophocrinidae that reduced the number of radial plates to four and lacked arms (Springer 1926a) (Fig. 1).

Although relatively little research on Paleozoic crinoids has considered eurytopy, range durations, and geographic distribution among crinoids, in a study of Mississippian crinoids, Kammer et al. (1997, 1998) concluded that Mississippian disparids were characterized by eurytopy and relatively long generic durations. Recently, Donovan et al. (2011) and Zamora et al. (2015) noted the unexpected cosmopolitan distribution of certain disparid genera during the Ordovician, which was a time characterized generally by endemic echinoderm faunas (Paul 1976; Lefebvre et al. 2013).

Disparid evolutionary history

The oldest disparid crinoid is *Alphacrinus* Guensburg (2010) from among the oldest known crinoid faunas in the middle Tremadocian of the Laurentia paleocontinent (Guensburg and Sprinkle 2003, 2009, 2010; Guensburg 2010). As early as the Floian, disparid crinoids had become geographically widespread with faunas present on the paleocontinents of Avalonia, Gondwana, and Laurentia

Editorial Handling: C. Klug.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s13358-018-0147-z) contains supplementary material, which is available to authorized users.

✉ William I. Ausich
ausich.1@osu.edu

[1] School of Earth Sciences, Ohio State University, 125 South Oval Mall, Columbus, OH 43210, USA

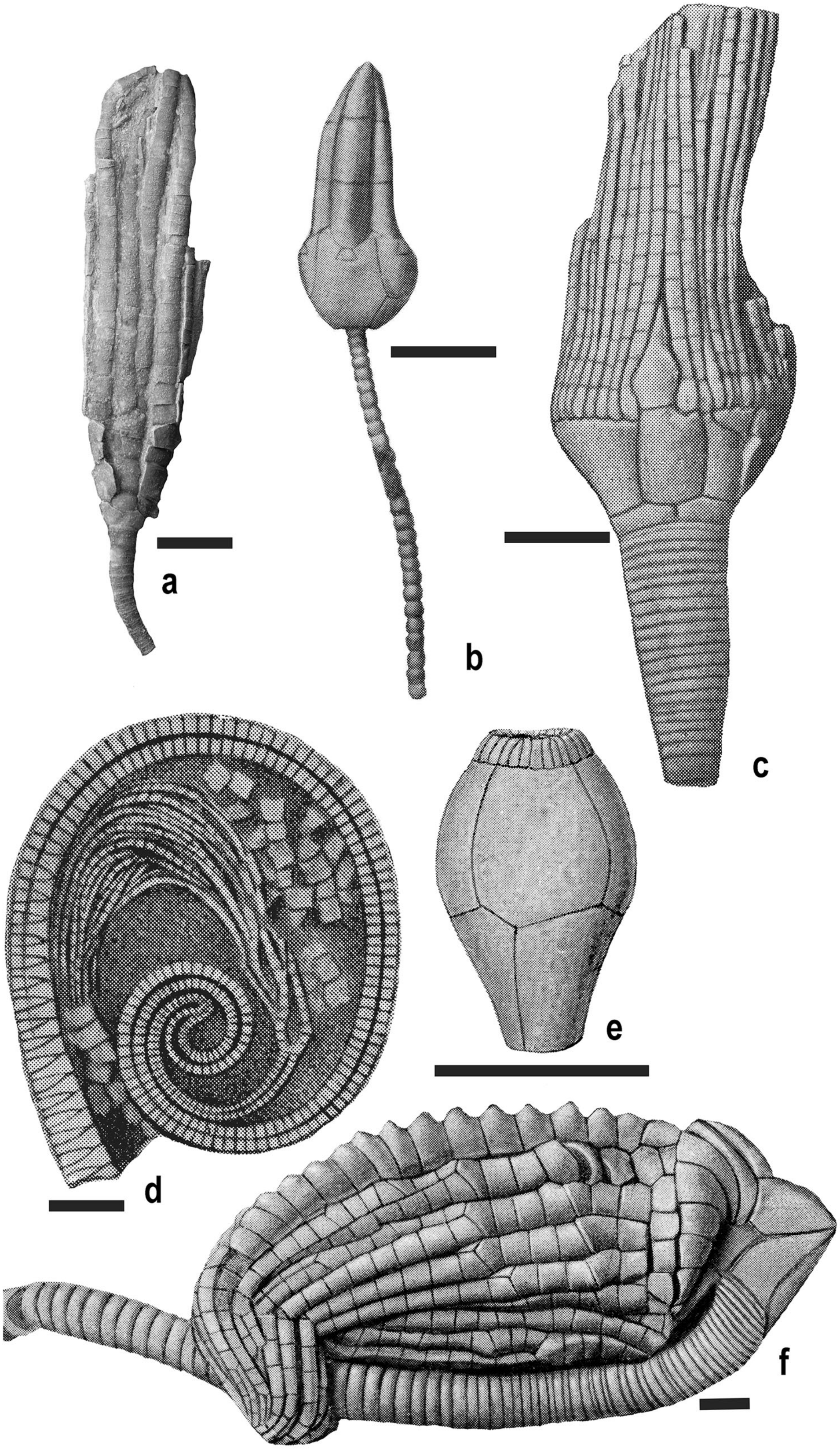


Fig. 1 Representative examples of members of the Parvclass Disparida: **a** lateral view of crown and proximal column of *Ectenocrinus simplex* (Hall 1847); OSU 54458; **b** lateral view of crown and proximal column of *Parapisocrinus quinquelobus* (Bather 1893); from Springer (1926a); **c** lateral view of crown and proximal column of *Catillocrinus tennesseeae* Shumard (1865); from Springer (1923); **d** lateral view of crown and proximal planispirally coiled column of *Myelodactylus extensus extensus* Springer (1926a); from Springer (1926b); **e** lateral view of aboral cup of *Zophocrinus howardi* Miller (1891) from Springer (1926a); **f** lateral view of crown and proximal column of the calceocrinid *Halysiocrinus tunicatus* (Hall 1860); from Springer (1926a). Scale bars 5 mm

(Kelly and Ausich 1978, 1979; Donovan 1988; Ausich 1986b; Guensburg and Waisfeld 2015). Despite wide distribution of a few taxa, disparids were largely endemic during the earlier Ordovician. Relative to other crinoids, disparids had the greatest biodiversity increase of any crinoid lineage during the Great Ordovician Biodiversity Event (GOBE) (Ausich and Deline 2012) (Fig. 2) and, along with diplobathrid camerates and hybocrinids, were the dominant crinoids of the Early Paleozoic Crinoid Evolutionary Fauna (Baumiller 1994; Ausich et al. 1994).

Genera and species diversified markedly during the Ordovician (Fig. 2), including 17 of the 30 disparid families that are traditionally recognized. This radiation also established the long-standing trend among disparids for extreme morphologies, including forms such as the acolocrinids with multiple very narrow arms on each radial plate, calceocrinids as noted above (Fig. 1f), and myelodactylids with the column planispirally coiled (Fig. 1d). Equally impressive to the Ordovician radiation was the severity of Late Ordovician extinctions (Eckert 1988; Donovan 1988, 1989a; Peters and Ausich 2008). Fewer than half of Ordovician genera and families survived into the Silurian (Fig. 2), and only two of these Ordovician families, Calceocrinidae and Pisocrinidae, attained much success thereafter (Ausich and Deline 2012).

Considering traditionally recognized families, five new families originated during the Silurian, seven new families originated during the Devonian, and one family originated during the Permian. No new disparid families emerged during the early Mississippian radiation that culminated in the “Age of Crinoids” (Kammer and Ausich 2006). This post-Ordovician history emphasizes further the contrasting role of disparids during the Ordovician versus the Silurian–Permian. Nevertheless, after the Ordovician, some extreme morphologies persisted, and new extreme morphologies originated. The Calceocrinidae is the longest ranging crinoid family (Late Ordovician to Middle Permian) and was quite diverse until the Late Devonian (see Ausich 1986b). After the Ordovician, the Pisocrinidae (Fig. 1b) and Myelodactylidae (Fig. 1d) also underwent a significant Silurian radiation, and additional originations of extreme morphologies included the Anamesocrinidae and Catillocrinidae (Fig. 1c) with multiple very narrow arms from each radial plate, the unusual Pygmaeocrinidae with very few brachialis forming a pyramidal cover over the oral surface, the Zophocrinidae that lacked arms (Fig. 1e), among others. The youngest known disparids are from the Middle Permian.

Previous work

The Treatise on Invertebrate Paleontology (Moore and Teichert 1978) was a seminal contribution to the study of crinoids and served as a springboard for the next generation of crinoid studies on morphology, paleoecology, systematics, and phylogeny. The Treatise understanding of disparid classification (Moore et al. 1978) and phylogeny (Lane 1978) was codified in Moore and Laudon (1943), and Moore (1952, 1962b). These authors used the number and position of compound radial plates, which define a plane of bilateral symmetry, as the primary criterion by which disparids can be subdivided (Fig. 3). Disparids are known with one, two, three, four, or five compound radial plates. Four basic types of disparid bilateral symmetry were defined by Ubaghs (1978, Fig. 43).

Although similarities exist, aspects of the Moore and Laudon (1943) and Lane (1978) phylogenies conflict. Moore and Laudon subdivided their Disparata into the Hybocrinidae and the homo-synbathocrinid stock. Their Disparata minus the Hybocrinidae (sensu Sprinkle and Moore 1978) are the Disparida of Moore and Teichert (1978), Wright et al. (2017), and the present study. Further, the discussion in Moore and Laudon (1943, pp. 24–29) does not align in all cases with their illustration (Moore and

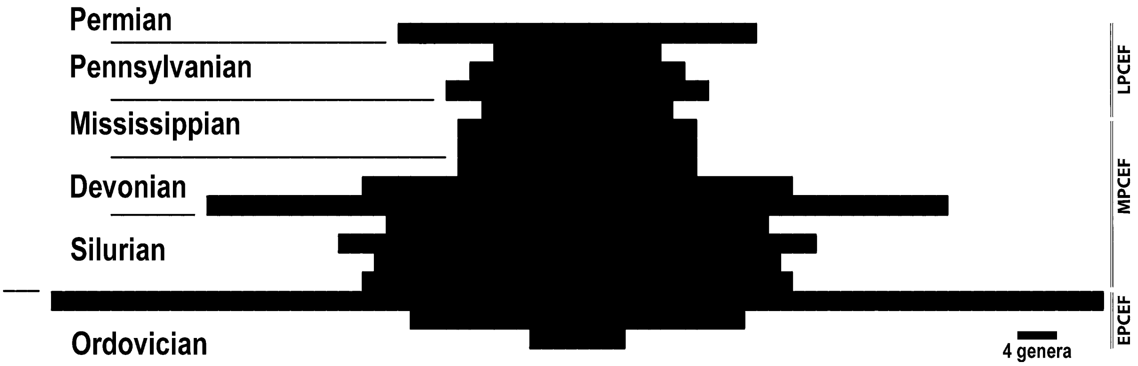


Fig. 2 Generic richness of the Parvclass Disparida through the Paleozoic. *EPCEF* Early Paleozoic Crinoid Evolutionary Fauna, *MPCEF* Middle Paleozoic Crinoid Evolutionary Fauna, and *LPCEF* Late Paleozoic Crinoid Evolutionary Fauna

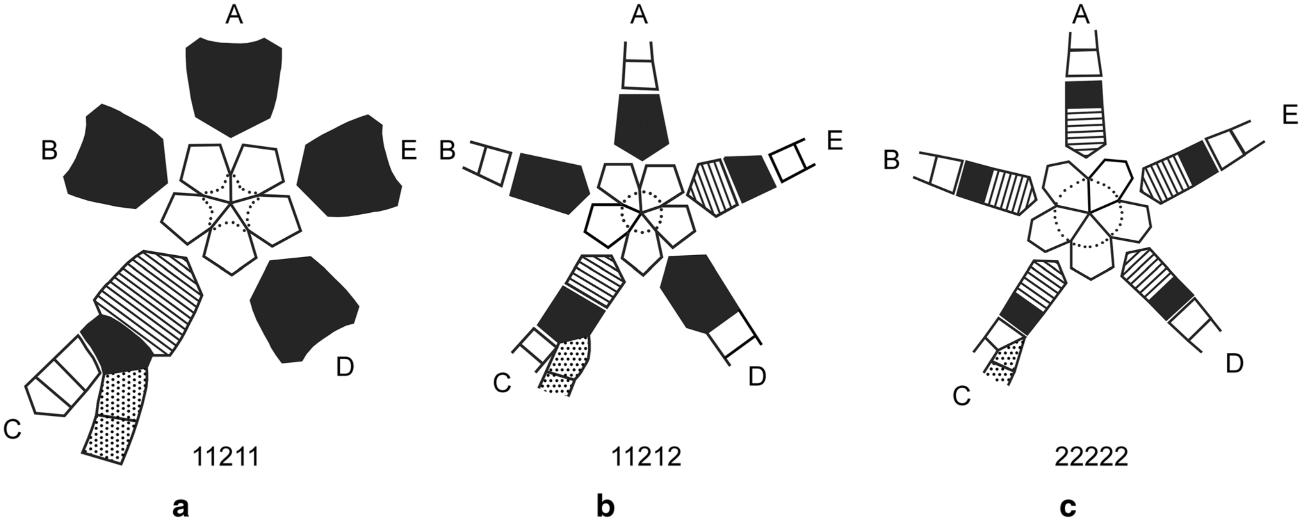


Fig. 3 Expanded plate diagrams for three disparid crinoids from an aboral view; radial circlet configuration given below each disparid, the order is A, B, C, D, and E, as explained in the text: **a** *Iocrinus subcrassus* with only the C ray with a compound radial plate; **b** two compound radial plates (C and E rays) in *Columbicrinus crassus*; **c** *Peniculocrinus milleri* with five compound radial plates. Radial plates and superradial plates filled with black shading; inferradial plates with horizontal ruling; posterior plates with stippled pattern, anal X plate indicated with an X; and arrows indicate position where brachials are fixed, if above the distal margin of the radial plate circlet. Not to scale

Laudon 1943, Fig. 3). An attempt to summarize the conclusions of these previous studies is given below.

The Eustenocrinidae, Iocrinidae, and Anomalocrinidae were regarded as having independent, deep origins; and the Eustenocrinidae was regarded as the most stemward group for the majority of disparids: "*Eustenocrinus* is probably not itself the ancestor of Middle Ordovician and younger homo-synbathocrinids, but this genus probably closely approximates the root of the stock" (Moore and Laudon 1943, p. 25). The Eustenocrinidae gave rise to the Homocrinidae, which in turn gave rise to most of the remaining disparids of the homo-synbathocrinid stock (Moore and Laudon 1943, Fig. 3).

Placing the Eustenocrinidae, which has five compound radial plates, in a stemward position was used undoubtedly in part as a consequence of selecting the disparid with the maximum number of plates in the aboral cup, thus the general overarching crinoid evolutionary trend of plate reduction could be invoked at the base of disparid evolutionary history (Moore 1952, p. 622; Lane 1978). Plate reduction is an important evolutionary trend within the Crinoidea, including the disparids, but plate addition was an equally important evolutionary trend, especially during the Early and Middle Paleozoic.

As noted, Lane (1978) also regarded the Eustenocrinidae as the most stemward disparid from which all other disparids arose. Three lineages emerged from the Eustenocrinidae, each defined by different aboral cup symmetries, including those with the homocrinoidal symmetry plane (E–BC), the heterocrinoidal symmetry plane (D–AB), and an imperfect crinoidal symmetry plane (A–CD). The Iocrinidae had the imperfect A–CD symmetry plane, and Lane (1978) derived the Myelodactylidae from the Iocrinidae. Those with a D–AB symmetry plane included the Heterocrinidae (now Cincinnaticrinidae) that questionably gave rise to the Anomalocrinidae. Those with the E–BC symmetry plane included the Homocrinidae that gave rise to the Calceocrinidae and at least some of the post-Ordovician groups, including the Synbathocrinidae and Belemnocrinidae (Lane 1978). *Tunguskocrinus* was identified as a potential ancestor for "at least some" post-Ordovician disparids. Lane (1978) did not speculate on the derivation of the Anamesocrinidae, Catillocrinidae, and Pisocrinidae. Lane (1978) did recognize several evolutionary trends among post-Ordovician crinoids, including fusion of infer- and superradial plates into simple radial plates, development of five atomous arms, and development of multiple very narrow atomous arms articulated to a single radial plate.

Ausich (1996, 1998a, b) also concluded that the eustenocrinid morphology represented the basal disparid from which four basic lineages emerged: Maennilicrinidae–Tetragonocrinidae, Homocrinidae–Calceocrinidae, Cincinnaticrinidae, and Iocrinidae–Myelodactylidae.

With discovery of the Tremadocian-aged *Alphacrinus*, Guensburg (2010, 2012) regarded this, the oldest disparid with some fixed interradial plates, as the most stemward disparid. From *Alphacrinus*, more tipward disparid taxa and clades included *Ibexocrinus*, *Iocrinus–Merocrinus–Isotomocrinus*, and *Ramseyocrinus–Tetragonocrinus*

(Guensburg 2012, Fig. 2). More recently in the analysis of early crinoid phylogeny (Ausich et al. 2015), the disparids, which form a clade, have either *Alphacrinus* or *Heviacrinus* as the most stemward disparid, depending on the taxa included in the analysis. In the analysis of only Tremadocian to Dapingian crinoids, *Alphacrinus* was at the base of the disparid clade (Ausich et al. 2015, Fig. 2a; and see below). Based on the results of Ausich et al. (2015), Wright (2017) and Wright et al. (2017), the disparids as a parvclass within the infraclass Inadunata and subclass Pentacrinoida.

Materials and methods

As indicated in the acknowledgments, studied material comes from specimens in numerous museums, as well as from the literature. The species included in analyses are listed in Online Resource 1a. Consistent with other 'Assembling the Echinoderm Tree of Life' projects (http://echinotol.org) (Ausich et al. 2015; Cole 2017; Wright 2017; Wright et al. 2017), disparids were initially coded with a rubric of 132 characters with a total of 568 potential character states (Ausich et al. 2015). For the present study, as possible, all Tremadocian through Darriwilian (Early through Middle Ordovician) disparid genera were coded; and as possible, representatives of all post-Ordovician families were included. A total of 100 disparids were coded, but only 80 characters were relevant for all disparids with fewer parsimony-informative characters applicable depending on the subset of taxa analyzed. Data are available on Morphobank (http://morphobank.org). The relatively small number of parsimony-informative characters, despite taxa with extreme morphology, is a consequence of disparids as a whole having relatively simple morphologies (Fig. 1a, b). Disparids are monocyclic (only radial and basal plate circlets in the aboral cup), fixed plates above the radial circlet are very uncommon, disparids are generally relatively small, and arms are either unbranched or typically have relatively simple branching. The relative dearth of discrete characters is especially acute for Silurian through Permian disparids as a whole.

Parsimony analyses were conducted in PAUP 4.0a142 (Swofford 2015) using the criterion of maximum parsimony. All characters were initially treated as equally weighted and unordered. Each analysis was a heuristic search with random addition that was repeated 1000 times. Branch swapping was performed using the tree bisection–reconnection (TBR) algorithm. Both strict consensus and 50% majority rule trees were evaluated, and Adams consensus trees were evaluated where appropriate to identify "wildcard taxa" for possible elimination (Wiley and Lieberman 2011). After initial analyses with unweighted characters, characters were weighted using the rescaled consistency indices (rc), and new trees were generated. The consistency index (ci), retention index (ri), and rescaled consistency index (rc) are presented for each tree. Bootstrap values and Bremer support were also calculated in PAUP 4.0a142. Additional details of the cladograms presented in this paper are in the figure captions and in the Online Resources.

Homology among crinoid calyx plates has been widely discussed (Moore 1962b; Ubaghs 1978; Simms 1993; Ausich 1996, 1998a, b; Rozhnov 2002; Guensburg and Sprinkle 2003; Wright 2015, 2017; Ausich et al. 2015; Guensburg et al. 2016; and others). The calyx plate homology scheme used here is taken basically from Ubaghs (1978). Analyses that accompanied Ausich et al. (2015) revealed that alternative homology schemes applied to the same calyx plate circlets did not affect the resulting topologies in phylogenetic analysis. One departure from the Ubaghs (1978) scheme that was used in this study is the coding of the C-ray aboral cup plates. In disparids, inferand superradial plates were coded rather than radial and anibrachials or brachianals (see Ausich 1996, 1998a; Ausich et al. 2015) in the C ray (Fig. 3a).

An exemplar species of each genus was used for phylogenetic analysis. Where possible, type species were coded, but in some cases other more completely understood species were coded (Online Resource 1a). *Alphacrinus* is used as the outgroup for analyses. As noted by Guensburg (2010), *Alphacrinus* is the oldest disparid and it retains some plesiomorphic characters. Also, as indicated in phylogenetic analysis of Tremadocian to Dapingian crinoids (Ausich et al. 2015, Fig. 2.4; Wright et al. 2017), the most stemward disparid was *Alphacrinus*. Alternatively, some analyses in Ausich et al. (2015) that included younger taxa placed *Heviacrinus* stemward of *Alphacrinus*. In the present study, *Alphacrinus* was used as the outgroup because of its position on cladograms in Ausich et al. (2015, Fig. 2a) and Wright (2017), because it is the oldest disparid (middle Temadocian) (compared to the Darriwilian-aged *Heviacrinus*), and because *Alphacrinus* retains fixed calyx plates in the interrays, as do Tremadocian crinoids in other clades (Guensburg and Sprinkle 2003, 2009, 2010; Guensburg 2010).

An important aspect of disparid morphology is the number and position of compound radial plates. Compound radial plates (biradials) are present in the majority of disparids. In the prototypical crinoid, a single radial plate (in a radial position) is sutured on the upper shoulders of two basal plates (each in an interradial position), and the arm is attached to the upper or distal margin of the radial plate (Fig. 3). A compound radial plate has two plates (inferradial plate and superradial plate) occupying the space where a single radial plate is typically present. The most common ray to have a compound radial plate is the C ray, but the full range of possibilities are realized from all five rays having compound radial plates to all five rays having simple radial plates (Fig. 3).

As discussed, the number and positions of compound radial plates are a character that unites many disparid clades, both in the traditional understanding of disparid phylogeny (Moore 1962b; Moore et al. 1978) as well as in some of the results described below. The following shorthand is used to designate the distribution of simple versus compound radial plates, 12212, and this is referred to herein as the radial circlet configuration. A radial circlet configuration of 12212 should be read as follows: simple radial plate in the A ray, compound radial plates in the B ray, compound radial plates in the C ray, simple radial plate in the D ray, and compound radial plates in the E ray (see Fig. 3).

A time-scaled phylogeny and stratigraphic congruence metrics were generated using the R package STRAP (Bell and Lloyd 2015). The congruence metrics include the Stratigraphic Consistency Index (SCI; Huelesbeck 1994), Relative Completeness Index (RCI; Benton and Storrs 1994), Manhattan stratigraphic measure (MSM*; Siddel 1988; Pol and Norell 2001), and gap excess ratio (GER; Willis 1999). Values for each metric were compared to a null model from a Monte Carlo simulation, thereby enabling determination of p values. The time-scaled phylogeny used a conservation method that constrains a node to be as old as its oldest descendant (Norell 1992; Smith 1994).

Preliminary equal-weight analysis of all coded disparids yielded a poorly resolved strict consensus tree with 8263 most parsimonious trees. Regardless, some traditionally recognized families are delineated as clades, as discussed below. In an attempt to better resolve disparid phylogenetic relationships, three methods (as in Ausich et al. 2015) were employed to obtain better resolved cladograms, including 1, removal of problematic taxa (those contributing to character conflict) from analysis; 2, a posteriori reweighting of characters based on their rescaled consistency indices (sensu Kroh and Smith 2010, as noted above); and 3, the stepwise stratigraphic sampling approach of Ausich (1998a, b). Taxa excluded from analyses were principally those with fewer than 70% of characters or those identified as a "wildcard" (Wiley and Lieberman 2011) in an Adams consensus tree (Supplemental Table 2).

The stepwise phylogenetic approach of Ausich (1998a, b) recognized that the branching at the base of a clade has historical consequences for the entire clade (Wagner 2000). However, the opposite may not be true. This is especially relevant for disparids, in which an iterative overarching morphology in many lineages is simplification of the calyx. In the stepwise approach, the oldest subset of taxa (Tremadocian–Darriwilian) is used to help constrain the base of the tree, and progressively younger taxa are analyzed to build on the initial phylogenetic structure. Accordingly, analyses are presented for Tremadocian through Darriwilian crinoids, Tremadocian through Sandbian taxa, Tremadocian through Katian taxa, all disparids, and only post-Ordovician disparids.

This study is only an analysis of phylogenetic relationships among disparid crinoids, as elucidated through parsimony analysis. A comprehensive classification for disparids will be proposed in a subsequent paper. Thus, taxa are referred herein to their currently recognized familial assignments, i.e., Moore et al. (1978) and Ausich (1998b), and subsequent publications (see Online Resource 1a).

Disparid phylogeny

As noted above, analysis of all coded taxa (with more than 70% of characters coded) yields a very poorly resolved consensus tree (8263 most parsimonious trees) (Fig. 4). Regardless, some families with specialized morphologies are sufficiently distinctive that they form clades despite the overall uncertainty of this cladogram. These distinctive families are the Acolocrinidae, Allagecrinidae, Anomalocrinidae, Belemnocrinidae, Calceocrinidae, Catillocrinidae, Eustenocrinidae, Myelodactylidae, and Pygmaeocrinidae. Other monophyletic groups are also presented in Fig. 4, but these either group taxa not traditionally recognized in the same family or group only some taxa from an otherwise larger family (again, as families are traditionally recognized). If the tree of Fig. 4 is analyzed with characters reweighted, nine most parsimonious trees are recognized, but with two exceptions (recognition of the Tetragonocrinidae, *Tetragonocrinus* and *Ramseyocrinus*; and loss of the Anomalocrinidae as a clade), the results (Online Resource 1c) are analogous to the clades identified in Fig. 4.

As noted, the above three methods were applied in an attempt to more definitively assess the phylogenetic relationships among disparids. Figure 5a is the single most parsimonious tree resulting from analysis of Tremadocian through Darriwilian disparids (note: only taxa used with more than 70% of characters coded, see Online Resource 1b). The analysis sorted taxa largely on the basis of the radial circlet configuration. Three of four iocrinids (11211 radial circlet configuration) form a clade; and with the fourth (*Schaldichocrinus*), the Iocrinidae are positioned as a grade between the outgroup, *Alphacrinus* (also with a 11211 radial circlet configuration), and all other more tipward disparids. *Othneiocrinus* (11212) is sister to all other tipward taxa. *Pogonipocrinus* and *Coralcrinus* (both eustenocrinids with a 22222 radial circlet configuration)

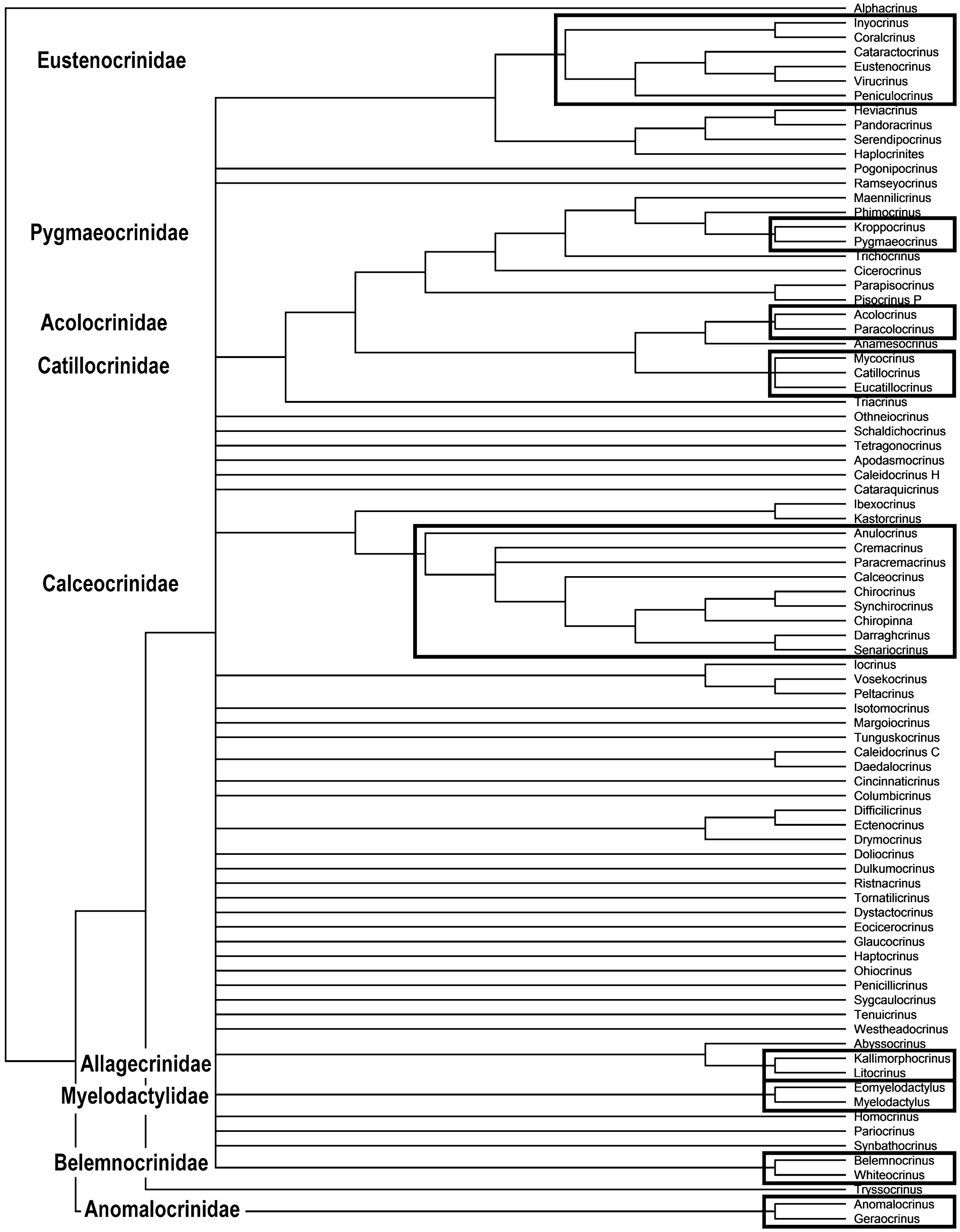


Fig. 4 Cladogram of all coded disparid crinoids; results from PAUP 4.0a142; heuristic search with random addition and 1000 repetitions, characters unweighted; strict consensus of 8263 most parsimonious trees, tree length 629, ci = 0.272, ri = 0.541, rc = 0.147

form a clade, as do *Ramseyocrinus* (11110) and *Tetragonocrinus* (01101) (note: both tetragonocrinids with a reduced number of radial plates and no compound radial plate). *Heviacrinus* (11111) is sister to *Ramseyocrinus* and *Tetragonocrinus*.

Isotomocrinus (11212, a cincinnaticrinid) is sister to the clade containing *Ramseyocrinus*, *Tetragonocrinus*, and *Heviacrinus*; and the remaining taxa (homocrinids; 12212) are aligned along a grade with *Cataraquicrinus* and *Apodasmocrinus* belonging to a more tipward clade, and

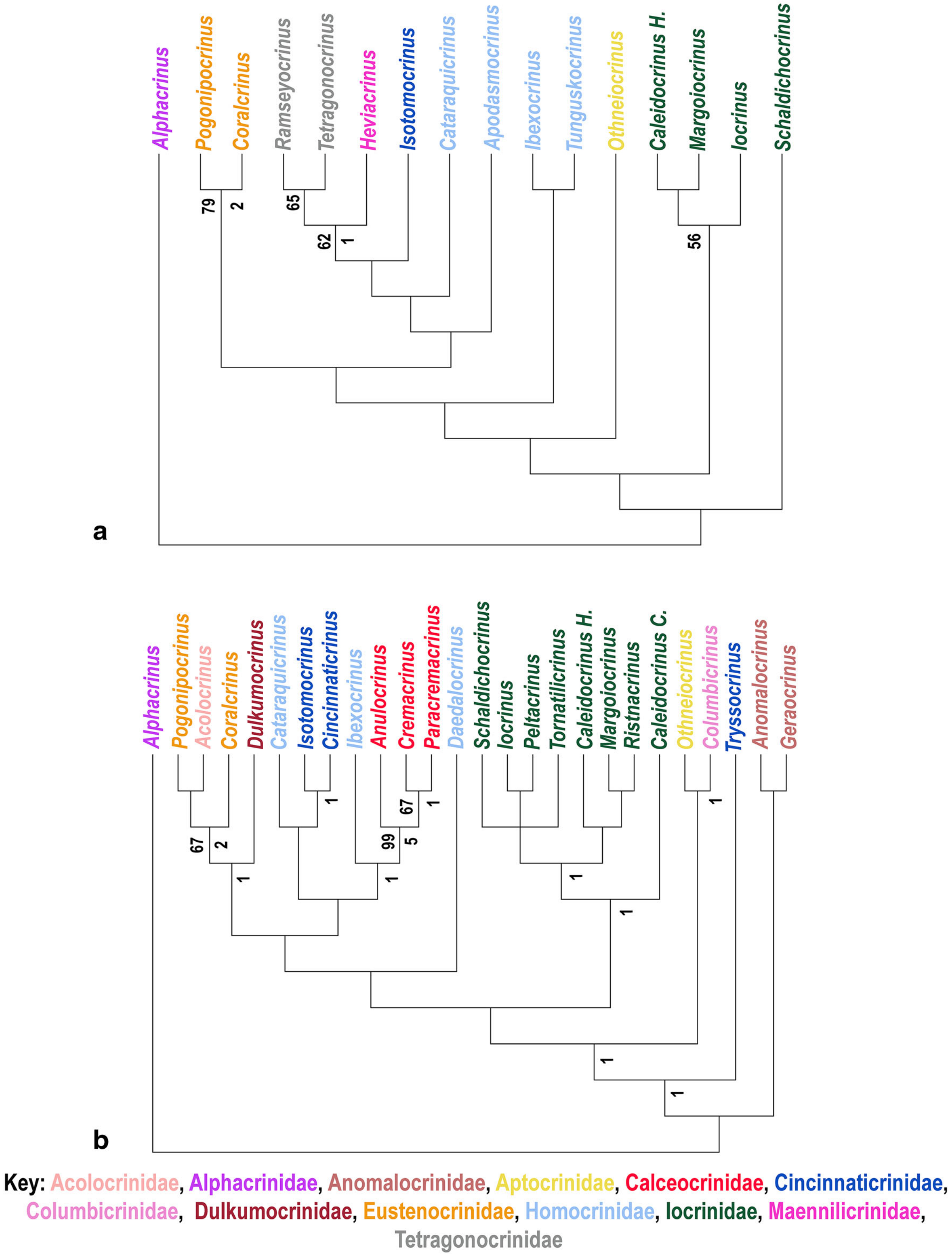


Fig. 5 Disparid cladograms from PAUP 4.0a142; both analyses resulted from heuristic search with random addition and 1000 repetitions (see Online Resource 1b for explanation of taxa excluded): **a** Tremadocian to Darriwilian cladogram, a posteriori reweighting of characters using their rescaled consistency indices, single most parsimonious tree, tree length 25.54, ci = 0.738, ri = 0.785, rc = 0.579. **b** Tremadocian to Sandbian cladogram, a posteriori reweighting of characters using their rescaled consistency indices, strict consensus of three most parsimonious trees, tree length 49.80, ci = 0.657, ri = 0.735, rc = 0.462. Bootstrap (left) and Bremer support (right) as appropriate for each clade

Ibexocrinus and *Tunguskocrinus* forming a separate clade. This cladogram unites taxa considered to be in each of the following families: Eustenocrinidae, Iocrinidae, and Tetragonocrinidae. Members of the Homocrinidae form a paraphyletic grade of taxa more tipward of the iocrinids.

Figure 5b is a strict consensus of the three most parsimonious trees that resulted from taking the taxa of Fig. 5a and adding genera representative of Sandbian-aged families. Note *Ramseyocrinus*, *Tetragonocrinus*, and *Heviacrinus* (Floian–Darriwillian taxa) are not included in Fig. 2a (Online Resource 1b); if included the tree resolution decreases when Sandbian taxa are included. The only polytomy in Fig. 5a is within the Iocrinidae, which is united as a clade.

Figure 5a, b is broadly congruent. In Fig. 5b, taxa with a 11212 radial circlet configuration form a grade from *Alphacrinus* to more tipward disparids. Two clades are identified in this grade: the Anomalocrinidae (*Anomalocrinus* and *Geraocrinus*) and a clade uniting *Othneiocrinus* (Aptocrinidae) and *Columbicrinus* (Columbicrinidae). *Tryssocrinus* (11212) is separated from other cincinnaticrinids. Two major monophyletic groups are present more tipward to this basal grade: one the Iocrinidae (11211) and the other all more tipward taxa. The clade sister to the Iocrinidae is comprised of three clades: Eustenocrinidae with Acolocrinidae (22222), the Calceocrinidae, (12212) and two (but not all) members of the Cincinnaticrinidae. Homocrinids are scattered throughout the clade sister to the iocrinid clade. The homocrinid *Daedalocrinus* (12212) is sister to the larger clade, homocrinid *Ibexocrinus* (12212) is sister to the Calceocrinidae clade, and the homocrinid *Cataraquicrinus* (12212) is sister to the more tipward cincinnaticrinids (11212). *Dulkumocrinus* (12222) is sister to the Eustenocrinidae/Acolocrinidae clade.

Figure 6a is the single most parsimonious tree from analysis of genera in Fig. 5b plus some Katian taxa. Although the single tree of Fig. 6a does not generally have strong support values, it is largely congruent with Fig. 5b. The well-defined clades Eustenocrinidae/Acolocrinidae, Calceocrinidae, and Anomalocrinidae are retained, as is the Iocrinidae (11211) that also includes *Othneiocrinus* (11211). The Anomalocrinidae retain their position immediately tipward of *Alphacrinus*. However, the paraphyletic Homocrinidae, Cincinnaticrinidae, and monogeneric families (Aptocrinidae, Columbicrinidae, and Dulkumocrinidae) are rearranged in this cladogram. The Anomalocrinidae, *Tyssocrinus* (cincinnaticrinid), and *Daedalocrinus* (homocrinid) form a paraphyletic grade immediately tipward of *Alphacrinus* and stemward of the Iocrinidae. *Othneiocrinus* (11212) is recovered in a derived position within the Iocrinidae (which is unlikely). The clade sister to iocrinids has a cincinnaticrinid (*Tenuicrinus*) and a homocrinid (*Penicillicrinus*) as a paraphyletic grade leading to two clades: one contains eustenocrinid/acolocrinid clade sister to the calceocrinids and the second is a miscellaneous group of para- and polyphyletic taxa. *Dystactocrinus* (cincinnaticrinid) is sister to the clade comprised of the eustenocrinids/acolocrinids and the calceocrinids. The eustenocrinid/acolocrinid and calceocrinid clades of Fig. 6a are congruent with Fig. 5b, with the exception that *Dulkumocrinus* is repositioned into the clade of miscellaneous taxa. This grouping of miscellaneous taxa, comprised of genera from several traditional families, has internal relationships that contrast with those of Fig. 5b, and this clade contains a mixture of cincinnaticrinids, columbicrinids, dulkumocrinid, homocrinids, and pisocrinids that does not display any particular phylogenetic structure.

Figure 7 considers disparids throughout the Paleozoic and is a single most parsimonious tree. Figure 7 is the result of analysis of all coded taxa with more than 70% of characters coded and characters reweighted (Online Resource 1b). This cladogram has many similarities with the relationships presented in Figs. 4, 5 and 6. For example, the Anomalocrinidae, Eustenocrinidae, Calceocrinidae, and Iocrinidae form clades. Different in Fig. 7 is that four homocrinids (*Ibexocrinus*, *Kastocrinus*, *Homocrinus*, and *Ectenocrinus*) form a distinct clade, and other taxa are also rearranged. The Belemnocrinidae (11111) and Calceocrinidae form very well supported clades. Rather than being within the clade that includes the Eustenocrinidae, Fig. 7 repositions *Acolocrinus* so that it forms a well-supported clade with the other member (*Paracolocrinus*) of the Acolocrinidae. The Acolocrinidae (22222) is joined with *Anamesocrinus* (12212) in a well-supported clade, which in turn is united in a well-supported clade with the Catillocrinidae (11111). This larger clade with the Catillocrinidae and Anamesocrinidae at its base unites disparids with multiple very narrow arms on individual radial plates, despite the fact that these taxa have contrasting radial circlet configurations.

All but two of the iocrinids remain in an Iocrinidae clade along with *Eomyelodactylus*. In contrast, Fig. 6a has *Othneiocrinus* nested within the iocrinid clade; but in Fig. 7 *Othneiocrinus* is sister to the clade with iocrinids and myelodactylids. The basal iocrinid in Figs. 5b and 6a, *Caleidocrinus* (*C.*), has shifted out of this clade to a more stemward position in Fig. 7; and the single Silurian iocrinid, *Pariocrinus*, is grouped with *Daedalocrinus* within the paraphyletic grade leading stemward to *Alphacrinus*.

Sister to the iocrinids is a clade subdivided into two major clades. Again, one of these clades contains the well-defined Eustenocrinidae and Calceocrinidae; but in contrast to Fig. 5b, this clade also contains the four-member clade of homocrinids noted above. *Penicillicrinus* (also a

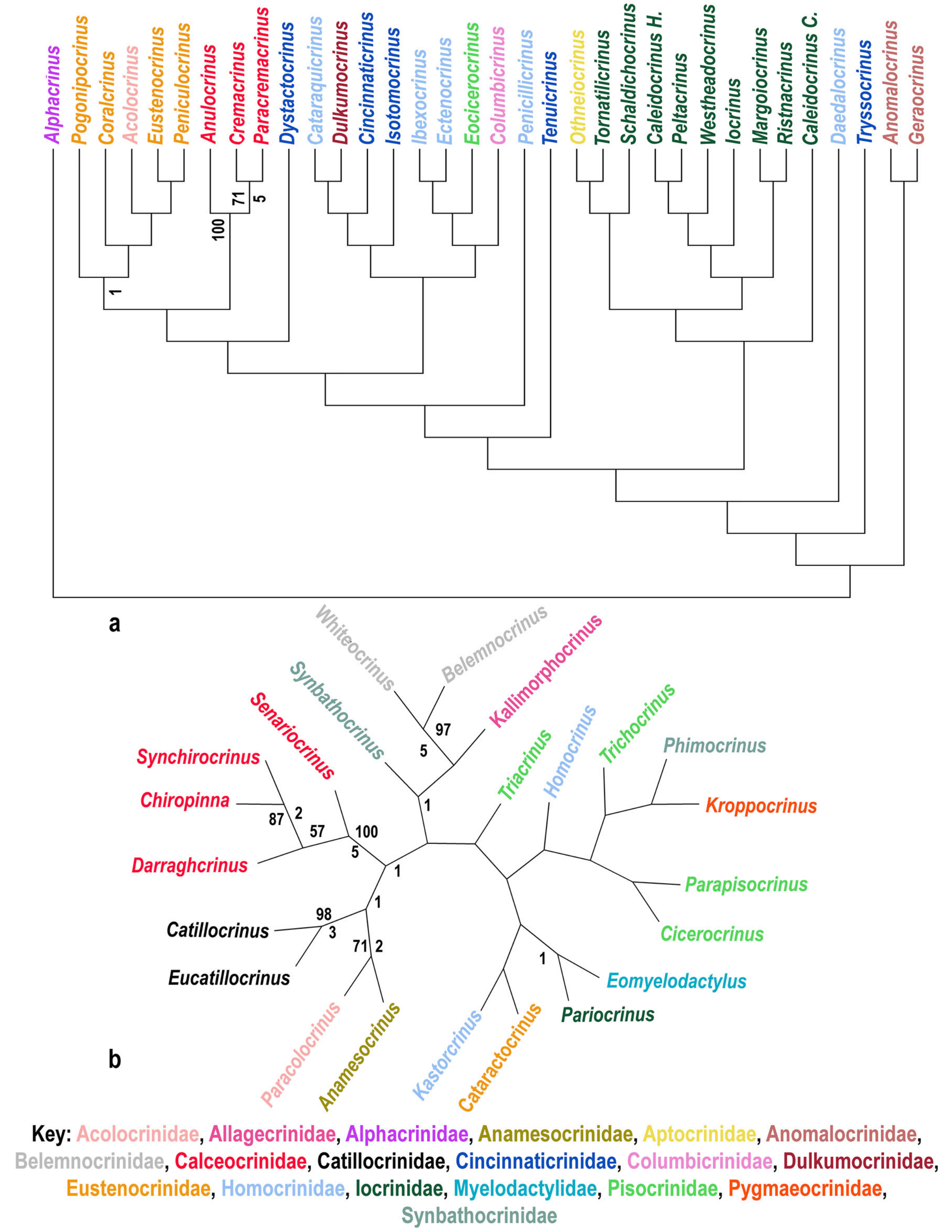


Fig. 6 Disparid cladograms from PAUP 4.0a142; both analyses resulted from heuristic search with random addition and 1000 repetitions, bootstrap (left) and Bremer support (right) as appropriate for each clade (see Online Resource 1b for explanation of taxa excluded): **a** Tremadocian to Katian cladogram, a posteriori reweighting of characters using their rescaled consistency indices, one most parsimonious tree, tree length 62.46, ci = 0.545, ri = 0.656, rc = 0.357; **b** unrooted cladogram of post-Paleozoic disparids, no a posteriori reweighting of characters, strict consensus of one most parsimonious tree, tree length 206, ci = 0.539, ri = 0.574, rc = 0.309. Bootstrap (left) and Bremer support (right) as appropriate for each clade

homocrinid) is the sister taxon of this larger clade, but the two other homocrinids (*Cataraquicrinus* and *Daedalocrinus*) are elsewhere in this cladogram.

The clade sister to the eustenocrinid/calceocrinid/"homocrinid" clade is comprised of two subclades. The first contains the acolocrinid/anamesocrinid/catillocrinid clade mentioned above and a sister clade comprised of pisocrinids and other taxa. *Eocicerocrinus* is most stemward in this clade, and *Phimocrinus* (11111, Synbathocrinidae, Silurian–Devonian) and *Kroppocrinus* (11111, Pygmaeocrinidae, Devonian) are nested among pisocrinids. As before, the remaining clade is a miscellaneous grouping of paraphyletic taxa, but this clade contains all but one cincinnaticrinid, one homocrinid, and *Dulkumocrinus*. This clade also contains *Synbathocrinus* (11111, Synbathocrinidae, Devonian–Permian) and *Allagecrinus* (11111, Allagecrinidae, Devonian–Pennsylvanian) as a clade. The two Belemnocrinidae are also united as a clade.

It is noteworthy that based on comparison to abnormal Devonian crinoids, McIntosh (1979) and Sevastopulo and Lane (1988) suggested that *Belemnocrinus* and *Whiteocrinus* are pseudomonocyclic, cladid crinoids that secondarily lost the infrabasal circlet. To test these suggestions, the taxa of Fig. 7, minus *Belemnocrinus* and *Whiteocrinus*, were analyzed to yield Online Resource 1d, which is a strict consensus of three trees. This tree is largely congruent with Fig. 7. The principle differences are with iocrinids and the paraphyletic homocrinids. In comparison to Fig. 7, Online Resource 1d includes *Caleidocrinus* (*C.*) in a clade with other iocrinids, but the position of *Pariocrinus* is unchanged. Finally, parallel to comparisons between other cladograms with different taxa considered, the position of genera within the Homocrinidae, Cincinnaticrinidae, and monogeneric families shifts.

Figure 6b is an unrooted tree of post-Ordovician disparids (taxa with more than 70% of characters coded, see Online Resource 1b) and is a single most parsimonious tree. The following relationships are congruent with other cladograms: Calceocrinidae form a well-supported group; Catillocrinidae form a well-supported group; the Catillocrinidae, Anamesocrinidae, and Acolocrinidae form a group; the Belemnocrinidae form a well-supported group; *Eomyelodactylus* is linked with the iocrinids (in this case *Pariocrinus*); *Kallimorphocrinus* and *Synbathocrinus* are in a group that includes the Belemnocrinidae; and *Phimocrinus* and *Kroppocrinus* are grouped with within the pisocrinids (whereas in Fig. 7 and Online Resource 1d, they are in a pisocrinid-dominated group but do not form a separate clade). Genera from the Ordovician holdover families, *Homocrinus* and *Kastorcrinus* (homocrinids) and *Cataractocrinus* (eustenocrinid), are scattered near the base of the large paraphyletic grouping dominated by pisocrinids. Note that if *Belemnocrinus* and *Whiteocrinus* are excluded from the analysis (Online Resource 1e), the overall tree topology does not change.

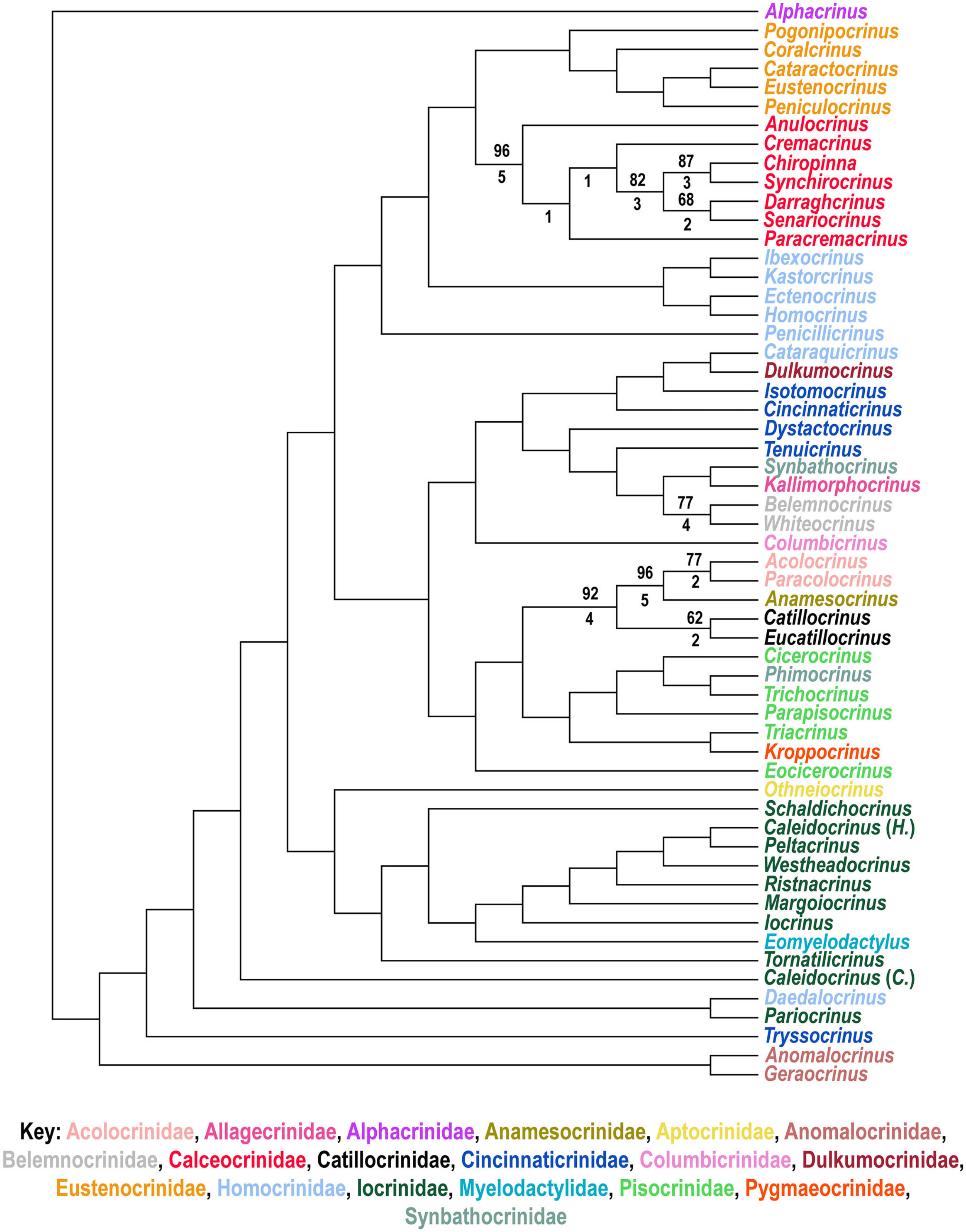
Finally, if post-Ordovician disparids with more than 60% of the characters coded are analyzed, most of relationships among genera remain consistent (Online Resource 1f). The relationships among calceocrinids and disparids with multiple armlets on each radial plate (*Acolocrinus*, *Paracolocrinus*, *Anamesocrinus*, *Catillocrinus*, and *Eucatillocrinus*) remain the same as in Figs. 6 and 7 (despite differences in the radial circlet configuration). The Myelodactylidae form a well-supported clade, and the two Allagecrinidae (*Kallimorphocrinus* and *Litocrinus*) form a clade. Countering expectations, many of the very simplified, five-armed disparids do not group in clades reflecting traditional familial assignments. *Pygmaeocrinus* (Pygmaeocrinidae) is in a reasonably well-supported clade with pisocrinids rather than with the other pygmaeocrinid (*Kroppocrinus*). *Kroppocrinus* is grouped with *Haplocrinites* (Haplocrinitidae). Also, the two synbathocrinids (*Phimocrinus* and *Synbathocrinus*) are positioned in different parts of the cladogram. If *Belemnocrinus* and *Whiteocrinus* are eliminated from the analysis (see explanation above), the branching pattern is altered somewhat (Online Resource 1g).

Discussion

The Disparida are a paradox, a combination of highly specialized and very simplified crinoids, which is demonstrated throughout the analyses presented herein. Some families, primarily the Homocrinidae and Cincinnaticrinidae, consistently and variously form polyphyletic groupings. However, regardless of the time slice considered, the taxa included, or the robustness of the coding for included taxa, the morphologically highly specialized clades emerge from a poorly resolved paraphyletic morass.

In previous studies (Moore and Laudon 1943; Moore 1952; Lane 1978; Ausich 1998a), the Eustenocrinidae were selected (or determined) to represent the most stemward disparid morphology. In the present analyses with *Alphacrinus* as the outgroup (Guensburg 2010), the eustenocrinids were a derived clade formed in part by the addition of compound radial plates in all rays.

The Acolocrinidae, Anomalocrinidae, Allagecrinidae, Belmnocrinidae, Calecocrinidae, Catillocrinidae, Eustenocrinidae, Myelodactylidae, and Tetragonocrinidae each consistently group their constituent taxa into clades. These families have traditionally been recognized as distinct by most previous authors based on their specialized morphologies and their radial circlet configuration (e.g., Moore


Alphacrinus
Pogonipocrinus
Coralcrinus
Cataractocrinus
Eustenocrinus
Peniculocrinus
Anulocrinus
Cremacrinus
Chiropinna
Synchirocrinus
Darraghcrinus
Senariocrinus
Paracremacrinus
Ibexocrinus
Kastorcrinus
Ectenocrinus
Homocrinus
Penicillicrinus
Cataraquicrinus
Dulkumocrinus
Isotomocrinus
Cincinnaticrinus
Dystactocrinus
Tenuicrinus
Synbathocrinus
Kallimorphocrinus
Belemnocrinus
Whiteocrinus
Columbicrinus
Acolocrinus
Paracolocrinus
Anamesocrinus
Catillocrinus
Eucatillocrinus
Cicerocrinus
Phimocrinus
Trichocrinus
Parapisocrinus
Triacrinus
Kroppocrinus
Eocicerocrinus
Othneiocrinus
Schaldichocrinus
Caleidocrinus (H.)
Peltacrinus
Westheadocrinus
Ristnacrinus
Margoiocrinus
Iocrinus
Eomyelodactylus
Tornatilicrinus
Caleidocrinus (C.)
Daedalocrinus
Pariocrinus
Tryssocrinus
Anomalocrinus
Geraocrinus
96
5
1
1
82
3
87
3
68
2
77
4
92
4
96
5
77
2
62
2
Key: Acolocrinidae, Allagecrinidae, Alphacrinidae, Anamesocrinidae, Aptocrinidae, Anomalocrinidae, Belemnocrinidae, Calceocrinidae, Catillocrinidae, Cincinnaticrinidae, Columbicrinidae, Dulkumocrinidae, Eustenocrinidae, Homocrinidae, Iocrinidae, Myelodactylidae, Pisocrinidae, Pygmaeocrinidae, Synbathocrinidae

◀**Fig. 7** Cladogram of Ordovician to Pennsylvanian disparids from PAUP 4.0a142; cladogram from heuristic search with random addition and 1000 repetitions after a posteriori reweighting of characters using their rescaled consistency indices; one most parsimonious tree, tree length 81.62, ci = 0.530, ri = 0.737, rc = 0.391 (see Online Resource 1b for explanation of taxa excluded); Bootstrap (above) and Bremer support (below) as appropriate for each clade

and Laudon 1943; Moore 1962b; Moore et al. 1978; Ausich 1998a; Guensburg 2012). Other traditionally recognized families that form clades in some analyses or examples where most of the constituent taxa typically form a clade include the Iocrinidae and Pisocrinidae. The radial circlet configuration appears to be a primary criterion that unites these taxa. In addition, some traditional views of families grouped into orders are supported by the results presented here. For example, the myelodactylids are nested within the iocrinids, which supports placement of these two groups in the Order Myelodactylida (Moore et al. 1978; Ausich 1998a) (Figs. 6b, 7); and despite the fact that *Eocicerocrinus* (Ordovician) has a different radial circlet configuration than other pisocrinids (all post-Ordovician), *Eocicerocrinus* may be positioned in a stemward placement relative to other pisocrinids, as envisioned by Donovan (1989b) (Fig. 7, Online Resource 1d).

One important contrast between Figs. 6a and 7 and Online Resource 1d is the position of *Acolocrinus*. *Acolocrinus* is within the Eustenocrinidae clade in Fig. 6a. In Fig. 7 the clade includes *Catillocrinus* (Mississippian–Pennsylvanian), *Eucatillocrinus* (Mississippian), *Anamesocrinus* (Devonian), *Acolocrinus* (Ordovician), and *Paracolocrinus* (Silurian), but the branching in this clade is in reverse stratigraphic order. In contrast, the oldest pisocrinid (*Eocicerocrinus*, Late Ordovician) is at the base of the pisocrinid clade; the older calceocrinids are positioned in the lower portion of the calceocrinid clade; and *Coralcrinus*, the oldest eustenocrinid in this analysis, is at the base of the eustenocrinid clade. Placement of *Synbathocrinus* versus *Phimocrinus* questions their status as confamilial genera. Although still a grade from *Alphacrinus* to more tipward taxa, the iocrinids retain some structure by being divided into two clades (Fig. 6a). *Eomyelodactylus*, the oldest member of the Myelodactylidae, is nested within the iocrinoids (all having a 11211 radial circlet configuration), and homocrinids and cincinnaticrinids are paraphyletic.

The limited taxa in the Tremadocian–Darriwilian analysis (Fig. 5a) are sorted reasonably well by radial circlet configuration; however, this pattern dissolves as younger taxa are included. Despite the consistency noted above for all well-defined clades, other families traditionally defined by the radial circlet configuration form inconsistent groupings and are typically members of paraphyletic groups. Among Ordovician or largely Ordovician families, the taxa from the Homocrinoidae and Cincinnaticrinidae lack consistent placement within clades. Members of these families are typically either at or near the basal branch of an otherwise well-defined clade or paired in a derived portion of the tree.

Columbicrinus and *Othneiocrinus* (Columbicrinidae and Aptocrinidae, respectively) may form a group (Fig. 5b). Alternatively, *Columbicrinus* may be in a stemward position in a paraphyletic clade (Figs. 6a, 7). *Othneiocrinus* may be stemward of the Iocrinidae or within the iocrinid grouping (Fig. 6a versus Fig. 7). *Cataraquicrinus* and *Dulkumocrinus* (Homocrinidae and Dulkumocrinidae, respectively) may be in different clades (Fig. 5b) or form a clade together with two cincinnaticrinids (*Cincinnaticrinus* and *Isotomocrinus*) (Figs. 6, 7).

Analyses were performed with only the simpler traditional families included (Online Resource 1h). These analyses included 24 taxa with only 32 parsimony-informative characters (fewer in analyses without the Iocrinidae included). As in previous analyses, iocrinids formed the stemward portion of the cladogram in all cases with homocrinids, cincinnaticrinids, and members of other families largely in a grade (some within clades) tipward of the iocrinids (Online Resource 1h). If column characters are excluded, the relative positions of some iocrinids change; tipward of iocrinids relative positions of taxa occur as well as some different taxa identified as clades; and *Eocicerocrinus* is positioned between iocrinids and other tipward taxa (Online Resource 1i). If iocrinids are eliminated from this analyses of (Online Resource 1j and 1k), the only insight into any phylogenetic structure is that *Othneiocrinus* and *Columbicrinus* form a clade (Fig. 5b).

Most post-Ordovician disparids are more difficult to evaluate. The Calceocrinidae and Pisocrinoidae are clades that originated during the Ordovician (assuming *Eocicerocrinus* is the most basal pisocrinid) and survived Late Ordovician extinctions. The relationships of families that originated after the Ordovician are more problematic because many have only simple radial plates (except the Anamesocrinidae and Haplocrinidae), all have atomous (unbranched) arms (except the Belemnocrinidae), and taxa have either five arms or multiple very narrow arms on each radial plate.

Families (as traditionally recognized) with post-Ordovician originations include the following (total range of families given): Allagecrinidae (11111) (Devonian to Permian), Anamesocrinidae (12212) (Devonian), Belemnocrinidae (11111) (Mississippian), Catillocrinidae (11111) (Devonian–Permian), Haplocrinitidae (12212) (Silurian to Mississippian), Holynocrinidae (10110) (Devonian), Paradoxocrinidae (11111) (Permian),

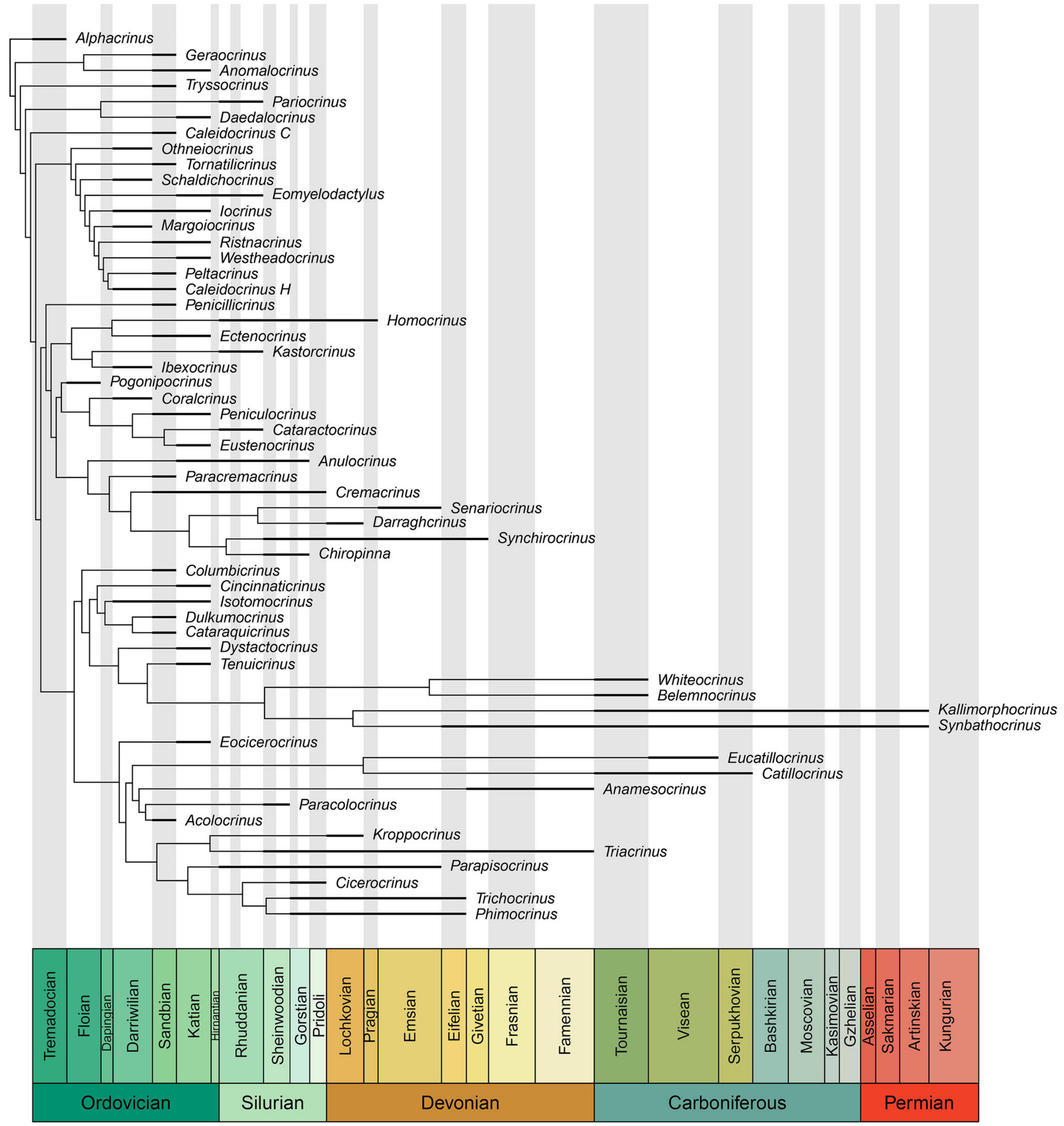


Fig. 8 Time-scaled tree based on Fig. 7. Tree constructed using DATEPHYLO function in STRAP (Bell and Lloyd 2015)

Pygmaeocrinidae (11111) (Silurian to Devonian), Quiniocrinidae (12211) (Devonian), Ramacrinidae (12212) (Silurian to Devonian), Synbathocrinidae (11111) (Silurian–Permian), and Zophocrinidae (11110) (Silurian–Devonian). Only members of the Allagecrinidae, Anamesocrinidae, Catillocrinidae, Pygmaeocrinidae, and Synbathocrinidae have taxa with a sufficient number of characters coded for phylogenetic analysis. Unfortunately, the following families lack a taxon that is well enough preserved to include in the analyses: Haplocrinitidae, Holynocrinidae, Paradoxocrinidae, Quiniocrinidae, Ramacrinidae, and Zophocrinidae.

Of the remaining families, the Allagecrinidae, Catillocrinidae, Pygmaeocrinidae, and Synbathocrinidae have a 11111 radial circlet configuration; and the Anamesocrinidae and Haplocrinitidae have a 12212 radial circlet

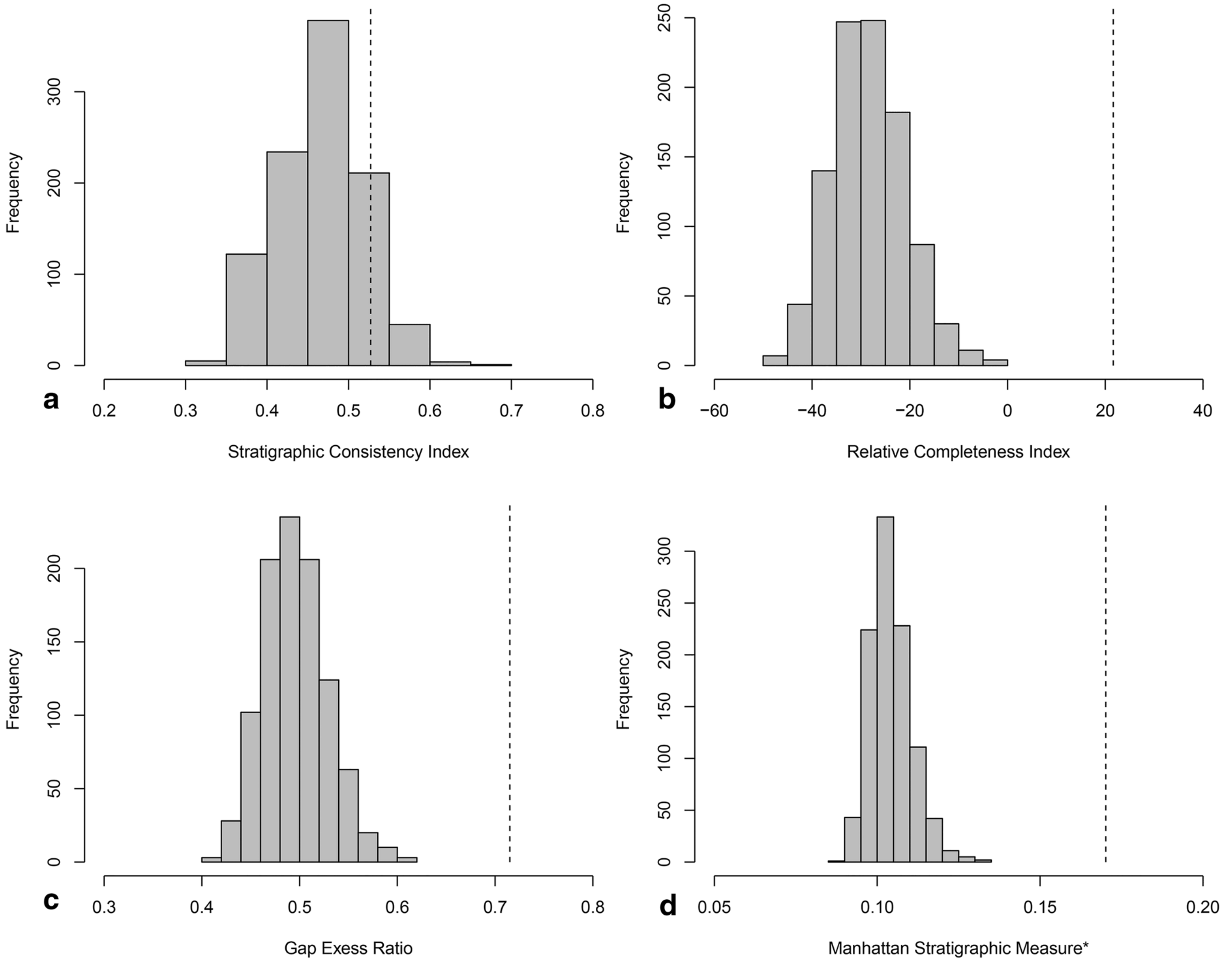


Fig. 9 Stratigraphic congruence analyses for the best fit phylogenetic distribution of Fig. 8. Dashed lines are observed values, and the histograms represent a null model produced with a Monte Carlo simulation from 1000 trees. *SCI* Stratigraphic Consistency Index (Huelesbeck 1994), *RCI* Relative Completeness Index (Benton and Storrs 1994), *MSM** Manhattan Stratigraphic Measure (Siddel 1988; Pol and Norell 2001), and GER, Gap Excess Ratio (Willis 1999)

configuration. If the poorly coded taxa are included in analyses of post-Ordovician disparids (Online Resource 1f and 1g; contrast with Fig. 6.2), the relationship of *Phimocrinus* and *Kroppocrinus* becomes unstable, with *Haplocrinites* (Haplocrinitidae) grouping with *Kroppocrinus* (Pygmaeocrinidae). However, most of the introduced taxa form a clade consistent with their traditional family assignments. For example, *Litocrinus* groups with *Kallimorphocrinus* (Allagecrinidae), *Myelodactylus* groups with *Eomyelodactylus* (Myelodactylidae), *Pisocrinus* (*Pisocrinus*) (Pisocrinidae) groups with other pisocrinids, and *Eocatillocrinus* and *Mycocrinus* group with other catillocrinids. However, also note that *Abyssocrinus* is positioned stemward of *Litocrinus* and *Kallimorphocrinus*, and *Pygmaeocrinus* groups with *Kroppocrinus*, which would not be anticipated.

Figure 8 is a time-scaled phylogeny based on the tree presented in Fig. 7. From this result, four stratigraphic congruence metrics were calculated (Fig. 9; Table 1). The dashed line on stratigraphic congruence histograms measures the stratigraphic congruence value for the tree in Fig. 7 compared to the null model generated for this tree. In three of four metrics, the topology of Figs. 7 and 8 was significantly different from random.

Conclusions

The parvclass Disparida is a well-defined clade. Paradoxically, the Disparida includes both some of the morphologically most simplified crinoids and some are clades comprised of some of the most morphologically specialized crinoids. Traditionally (Moore and Laudon 1943;

Table 1 Summary statistics for stratigraphic congruence significance tests of the best phylogenetic hypothesis

Stratigraphic congruence measure	Calculated value	*p* value
Stratigraphic Consistency Index	0.527	1.2×10^{-1}
Relative Consistency Index	21.6	1.9×10^{-11}
Gap excess ratio	0.715	4.6×10^{-12}
Manhattan stratigraphic measure	0.17	3.3×10^{-21}

Moore 1952; Lane 1978; Ausich 1998a), the positions and number of compound radial plates was a foundational basis for the disparid phylogenetic tree; but based on analyses presented here, this does not dominate the phylogeny of all disparids. The specialized clades typically have the same radial circlet configuration, but these clades largely arose from a paraphyletic collection of simplified taxa belonging to different traditionally defined families. With *Alphacrinus* as the outgroup, the Iocrinidae form a paraphyletic grade to more tipward disparids. Two primary clades are tipward of the iocrinids: one with pisocrinids as largely basal and the other largely with paraphyletic cincinnaticrinids and homocrinids basal. Families of highly specialized disparids (e.g., Acolocrinidae, Calceocrinidae, Catillocrinidae, and Myelodactylidae) consistently form well-supported clades, as do some distinctive forms (e.g., Allagecrinidae, Eustenocrinidae, and Tetragonocrinidae). Primary questions raised by these analyses include whether multiple very narrow arms on a single radial plate is a morphology that evolved more than once; what is the phylogenetic relationship among and between the Homocrinidae and Cincinnaticrinidae; determination of the phylogenetic position of several post-Ordovician forms that have either simplified morphology (e.g., *Kroppocrinus* and *Phimocrinus*) or too few characters to include in numerical analyses (e.g., *Zophocrinus* and *Paradoxocrinus*); and how should superfamilial clades be recognized. Finally, given the relative dearth of parsimony-informative characters for the disparids with very simple morphology, to what degree can a strictly phylogenetic classification be constructed using the parsimony results presented herein.

Acknowledgements S.R. Cole ran the analyses for the time-scaled tree and the stratigraphic congruence metrics. S.R. Cole, D.F. Wright, E.C. Rhenberg, and T.W. Kammer are also thanked for improving preliminary drafts of this manuscript and/or for discussions of various ideas leading to this manuscript. Careful reviews by two anonymous reviewers significantly improved this manuscript. Also, we thank the following (in alphabetical order) for assistance with curated specimens: Tiffany Adrain, University of Iowa; Roger Burkhalter, Sam Noble Oklahoma Museum of Natural History University of Oklahoma; Jessica Cundiff, Museum of Comparative Zoology, Harvard University; Jean Dougherty, Geological Survey of Canada, Ottawa; Tim Ewin, Natural History Museum, London; Kathy Hollis, US National Museum of Natural History; Brenda Hunda Cincinnati Museum Center; Kathy Leacock, Buffalo Museum of Science; Franz-Josef Lindemann, Natural History Museum, University of Oslo; Paul Mayer, Field Museum of Natural History; Ann Molineux, University of Texas, Austin; Sergey Rozhnov and G.V. Mirantsev, Borissiak Paleontological Institute, Moscow; Janet Waddington, Royal Ontario Museum. David Swofford made PAUP 4.0a142 available for this research. This research was supported by the US National Science Foundation project Assembling the Echinoderm Tree of Life (DEB 1036416).

References

Ausich, W. I. (1986a). Palaeoecology and history of the Calceocrinidae (Palaeozoic Crinoidea). *Palaeontology, 29,* 85–99.

Ausich, W. I. (1986b). The crinoids of the Al Rose Formation (Early Ordovician, Inyo County, California, USA). *Alcheringa, 10,* 217–224.

Ausich, W. I. (1996). Crinoid plate circlet homologies. *Journal of Paleontology, 70,* 955–964.

Ausich, W. I. (1998a). Early phylogeny and subclass division of the Crinoidea (phylum Echinodermata). *Journal of Paleontology, 72,* 499–510.

Ausich, W.I. (1998b). *Phylogeny of Arenig to Caradoc Crinoids (Phylum Echinodermata) and suprageneric classification of the Crinoidea.* University of Kansas Paleontological Contributions Papers, New Series, 9, 36 pp.

Ausich, W. I., & Deline, B. (2012). Macroevolutionary transition in crinoids following the Late Ordovician extinction event (Ordovician to Early Silurian). *Palaeogeography, Palaeoclimatology, Palaeoecology, 361–362,* 38–48. https://doi.org/10.1016/j.palaeo.2012.07.022.

Ausich, W. I., Kammer, T. W., & Baumiller, T. K. (1994). Demise of the Middle Paleozoic crinoid fauna: A single extinction event or rapid faunal turnover? *Paleobiology, 20,* 345–361.

Ausich, W. I., Kammer, T. W., Rhenberg, E. C., & Wright, D. F. (2015). Early phylogeny of crinoids within the Pelmatozoan clade. *Palaeontology, 58,* 937–952.

Bather, F.A. (1893). *The Crinoidea of Gotland, Part 1: The Crinoidea Inadunata*. Kongliga Svenska Vetenskaps-Adademiens Handlingar, 25(2), 200 pp.

Baumiller, T. K. (1994). Patterns of dominance and extinction in the record of Paleozoic crinoids. In B. David, A. Guille, J. P. Féral, & M. Roux (Eds.), *Echinoderms Through Time (Echinoderms Dijon)* (pp. 193–198). Rotterdam: A. A. Balkema.

Bell, M. A., & Lloyd, G. T. (2015). STRAP: An R package for plotting phylogenies against stratigraphy and assessing their stratigraphic congruence. *Palaeontology, 58,* 379–389.

Benton, M. J., & Storrs, G. W. (1994). Testing the quality of the fossil record: Paleontological knowledge is improving. *Geology, 22,* 111–114.

Brower, J. C. (1966). Functional morphology of Calceocrinidae with description of some new species. *Journal of Paleontology, 40,* 613–634.

Cole, S. R. (2017). Phylogeny and morphologic evolution of the Ordovician Camerata (Class Crinoidea, Phylum Echinodermata). *Journal of Paleontology, 91,* 715–734.

Donovan, S. K. (1988). The early evolution of the Crinoidea. In C. R. C. Paul & A. B. Smith (Eds.), *Echinoderm phylogeny and evolutionary biology* (pp. 235–244). Oxford: Clarendon Press.

Donovan, S. K. (1989a). The significance of the British Ordovician crinoid fauna. *Modern Geology, 13,* 243–255.

Donovan, S. K. (1989b). Pelmatozoan columnals from the Ordovician of the British Isles, Part 2. *Palaeontographical Society Monograph, 142*(580), 60–114.

Donovan, S. K., Miller, C. G., Sansom, I. J., Heward, A. P., & Schreurs, J. (2011). A Laurentian *Iocrinus* Hall (Crinoidea, Disparida) in the Dapingian or Darriwilian (Middle Ordovician, Arenig) of Oman. *Palaeontology, 54,* 525–533.

Eckert, J. D. (1988). Late Ordovician extinction of North American and British crinoids. *Lethaia, 21,* 147–167.

Guensburg, T. E. (2010). *Alphacrinus* new genus and origin of the disparid clade. *Journal of Paleontology, 84,* 1209–1216.

Guensburg, T. E. (2012). Phylogenetic implications of the oldest crinoids. *Journal of Paleontology, 86,* 455–461.

Guensburg, T. E., Blake, D. B., Sprinkle, J., & Mooi, R. (2016). Crinoid ancestry without blastozoans. *Acta Palaeontologica Polonica, 61,* 253–266.

Guensburg, T. E., & Sprinkle, J. (2003). The oldest known crinoids (Early Ordovician, Utah) and a new crinoid plate homology system. *Bulletins of American Paleontology, 364,* 43.

Guensburg, T. E., & Sprinkle, J. (2009). Solving the mystery of crinoid ancestry: New fossil evidence of arm origin and development. *Journal of Paleontology, 83,* 350–374.

Guensburg, T. E., & Sprinkle, J. (2010). Emended restoration of *Titanocrinus sumralli* Guensburg and Sprinkle, 2003 (Echinodermata, Crinoidea). *Journal of Paleontology, 84,* 566–568.

Guensburg, T. E., & Waisfeld, B. (2015). South America's earliest (Ordovician, Floian) crinoids. *Journal of Paleontology, 89,* 622–630.

Hall, J. (1847). *Palaeontology of New York, v. 1, Containing descriptions of the organic remains of the lower division of the New-York system (equivalent of the Lower Silurian rocks of Europe)*. Natural History of New York. Albany, State of New York, 6, 338 pp.

Hall, J. (1852). *Crinoidea of the Clinton and Niagara Groups (equivalent, in part, of the Middle Silurian strata of Europe)*. Albany, 72 pp.

Huelesbeck, J. P. (1994). Comparing the stratigraphic record to estimates of phylogeny. *Paleobiology, 20,* 470–483.

Kammer, T. W., & Ausich, W. I. (2006). The "Age of Crinoids": A Mississippian biodiversity spike coincident with widespread carbonate ramps. *Palaios, 21,* 238–248.

Kammer, T. W., Baumiller, T. K., & Ausich, W. I. (1997). Species longevity as a function of niche breadth: Evidence from fossil crinoids. *Geology, 25,* 219–222.

Kammer, T. W., Baumiller, T. K., & Ausich, W. I. (1998). Evolutionary significance of differential species longevity in Osagean–Meramecian (Mississippian) crinoid clades. *Paleobiology, 24,* 155–176.

Kelly, S. M., & Ausich, W. I. (1978). A new Lower Ordovician disparid crinoid from Utah. *Journal of Paleontology, 52,* 916–920.

Kelly, S. M., & Ausich, W. I. (1979). A new name for the Lower Ordovician crinoid *Pogocrinus* Kelly and Ausich. *Journal of Paleontology, 53,* 1433.

Kroh, A., & Smith, A. B. (2010). The phylogeny and classification of post-Paleozoic echinoids. *Journal of Systematic Palaeontology, 8,* 147–212.

Lane, N.G. (1978). Disparida and Hybocrinida. R.C. Moore, & C. Teichert (Eds.), *Treatise on invertebrate paleontology, Pt. T. Echinodermata, 2,* Volume 2 (pp. T292–T294). Boulder, Colorado and Lawrence, Kansas: Geological Society of America and University of Kansas Press.

Lefebvre, B., Sumrall, C.D., Shroat-Lewis, R.A., Reich, M., Webster, G.D., Hunter, A.W., Nardin, E., Rozhnov, S.V., Guensburg, T.E., Touzeau, A., Noailles, F., & Sprinkle, J. (2013). Palaeobiogeography of Ordovician echinoderms. In D.A.T. Harper, & T. Servais (Eds.), *Early palaeozoic biogeography and palaeogeography* (pp. 173–198). Geological Society, London Memoirs, 38.

McIntosh, G. (1979). Abnormal specimens of the Middle Devonian crinoid *Bactrocrinites* and their effect on the taxonomy of the genus. *Journal of Paleontology, 53,* 18–28.

Miller, S.A. (1891). *Palaeontology*. Advance Sheets, Indiana Department of Geology and Natural Resources, 17th Annual Report, 103 pp.

Moore, R.C. & L.R. Laudon. (1943). *Evolution and classification of Paleozoic crinoids*. Geological Society of America, Special Paper 46, 151 pp.

Moore, R. C. (1952). Crinoids. In R. C. Moore, C. G. Lalicker, & A. G. Fischer (Eds.), *Invertebrate fossils* (pp. 604–652). New York: McGraw-Hill Book Company Inc.

Moore, R.C. (1962a). *Revision of Calceocrinidae*. University of Kansas Paleontological Contributions, Echinodermata Article, 4, 40 pp.

Moore, R. C. (1962b). *Ray structures of some Inadunate crinoids*. University of Kansas, Paleontological Contributions, Echinodermata Article, 5, 47 pp.

Moore, R.C., & C. Teichert (Eds). (1978). *Treatise on invertebrate paleontology, Part T, Echinodermata 2, Crinoidea*, 3 volumes. Boulder Colorado and Lawrence, Kansas: Geological Society of America and University of Kansas, 1027 pp.

Moore, R.C., Lane, N.G., Strimple, H.L., & Sprinkle, J. (1978). Order Disparida Moore and Laudon, 1943. In R.C. Moore, & C. Teichert (Eds.), *Treatise on invertebrate paleontology, Part T, Echinodermata 2, Crinoidea* (pp. T520–T564). Boulder Colorado and Lawrence Kansas: Geological Society of America and University of Kansas, pp. T520–T564.

Norell, M. A. (1992). Taxic origin and temporal diversity: The effect of phylogeny. In M. J. Novacek & Q. D. Wheeler (Eds.), *Extinction and phylogeny* (pp. 89–118). New York: Columbia University Press.

Paul, C.R.C. (1976). Palaeogeography of primitive echinoderms in the Ordovician. In M. G. Bassett (Ed.), *The Ordovician system*. Proceedings of a Palaeontological Association symposium, Birmingham, September, 1974 (pp. 533–574). Cardiff: University of Wales Press,

Peters, S. E., & Ausich, W. I. (2008). A sampling-adjusted macroevolutionary history for Ordovician-Early Silurian crinoids. *Paleobiology, 34,* 104–116.

Phillips, J. (1836). *Illustrations of the geology of Yorkshire, or a description of the strata and organic remains. Pt 2, The Mountain Limestone districts* (2nd ed., pp. 203–208). London: John Murray.

Pol, D., & Norell, M. A. (2001). Comments on the Manhattan stratigraphic measure. *Cladistics, 17,* 285–289.

Rozhnov, S. V. (2002). Morphogenesis and evolution of crinoids and other Pelmatozoan echinoderms in the early Paleozoic. *Palaeontological Journal, 36*(sup. to issue 6), S525–S674.

Sevastopulo, G. D., & Lane, N. G. (1988). Ontogeny and phylogeny of disparid crinoids. In C. R. C. Paul & A. B. Smith (Eds.), *Echinoderm phylogeny and evolutionary biology* (pp. 245–253). Oxford: Clarendon Press.

Shumard, B. F. (1865). Catalogue of Palaeozoic fossils, Part 1, Echinodermata. *Transactions of the St. Louis Academy of Science, 2*(2), 334–407.

Siddel, M. E. (1988). Stratigraphic fit to phylogenetics: a proposed solution. *Cladistics, 14,* 201–208.

Simms, M. J. (1993). Reinterpretation of thecal plate homology and phylogeny in the Class Crinoidea. *Lethaia, 26,* 303–312.

Smith, A. B. (1994). *Systematics and the fossil record. Documenting evolutionary patterns* (p. 223). Oxford: Blackwell Science.

Springer, F. (1923). *On the fossil crinoid family Catillocrinidae*. Smithsonian Miscellaneous Collection, 76, 239 pp.

Springer, F. (1926a) *American Silurian crinoids*. Smithsonian Institution Publication, 2872, 239 pp.

Springer, F. (1926b). *Unusual forms of fossil crinoids*. Proceedings of the US National Museum, 67, 137 pp.

Sprinkle, J., & Moore, R.C. (1978). Hybocrinida. In Moore, R.C. & Teichert, C. (Eds.), *Treatise on Invertebrate Paleontology, Pt. T. Echinodermata, 2, Volume 2* (pp. T564–T574). Boulder, Colorado and Lawrence Kansas: Geological Society of America and University of Kansas Press.

Swofford, D.L. (2015). PAUP*: Phylogenetic analysis using parsimony (and other methods) (version 4.0a142).

Ubaghs, G. (1978). Skeletal morphology of fossil crinoids. In R.C. Moore, & C. Teichert (Eds.), *Treatise on Invertebrate Paleontology, Pt. T. Echinodermata, 2, Volume 2* (pp. T58–T216). Boulder, Colorado and Lawrence, Kansas: Geological Society of America and University of Kansas Press.

Wagner, P. L. (2000). Exhaustion of morphological character states among fossil taxa. *Evolution, 54,* 365–386.

Wiley, E. O., & Lieberman, B. S. (2011). *Phylogenetics: Theory and practice of phylogenetics* (p. 432). Hoboken: Wiley-Blackwell.

Willis, M. A. (1999). Congruence between phylogeny and stratigraphy: randomization tests and the Gap Excess Ratio. *Systematic Biology, 48,* 559–580.

Wright, D. F. (2015). Fossils, homology, and "Phylogenetic Paleontogeny": a reassessment of primary posterior plate homologies among fossil and living crinoids with insights from developmental biology. *Paleobiology, 4,* 570–591.

Wright, D. F. (2017). Baysian estimation of fossil phylogenies and evolution of early to middle Paleozoic crinoids (Echinodermata). *Journal of Paleontology, 91,* 799–814.

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

Zamora, S., Rahman, I. A., & Ausich, W. I. (2015). A new iocrinid crinoid (Disparida) from the Ordovician (Darriwilian) of Morocco. *PeerJ, 3,* e1450. https://doi.org/10.7717/peerj.1450.