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PHYLOGENY OF ARENIG TO CARADOC CRINOIDS (PHYLUM ECHINODERMATA) AND SUPRAGENERIC CLASSIFICATION OF THE CRINOIDEA

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Abstract.—Stepwise, parsimony-based character analysis of Arenig to Caradoc crinoids (Ordovician) indicates that Early and middle Ordovician crinoids represent a radiation largely confined to the Ordovician. Only a few middle Paleozoic families are considered to have roots among these Early and middle Ordovician genera. Also, most genera are reinterpreted as a part of larger Ordovician clades rather than being isolated in monogeneric families.

Six subclasses recognized as a result of phylogenetic analysis are the Aethocrinea, Cladida, Flexibilia, Articulata, Camerata, and Disparida. Many aspects of the *Treatise* classification (Moore and Teichert, 1978) are followed, but significant differences exist. The zygodiplobathrid-eudiplobathrid camerate suborder distinction is not made, and disparid superfamilies are no longer recognized. The subclass Disparida is subdivided into orders rather than superfamilies. Seven Early and middle Ordovician disparid orders are recognized, and additional younger orders undoubtedly exist. Whereas disparid superfamilies in the *Treatise* were defined largely on aboral cup symmetry, disparid orders are defined here largely on the basis of presence and absence of radial plates and aboral cup architecture. The Calceocrinida, Homocrinida, Myelodactylida, Eustenocrinida, and Tetragonocrinida are new orders, having previously been regarded as superfamilies and subfamilies; the Maennilicrinida is a new order; and the order Hybocrinida is maintained in the subclass Disparida. Subfamilies are no longer recognized within the Homocrinidae or Cincinnaticrinidae.

Other changes include new families (Agostocrinidae, Columbicrinidae, and Maennilicrinidae), one family elevated from subfamily to family (Atopocrinidae), and reassignment of families to different higher categories (Acolocrinidae to the Eustenocrinida, Agostocrinidae and Colpodecrinidae to the Cladida, Cleiocrinidae to the Rhodocrinitacea, and Porocrinidae to the Cyathocrinitacea). Reassignment of 34 genera to different families is proposed (3 of these to a different subclass). A number of family-level taxa are recognized as junior synonyms and *Baerocrinus, Ontariocrinus,* Baerocrinidae, and Ontariocrinidae are regarded as *nomina dubia.*

INTRODUCTION

Ausich (1995, 1996a) proposed a new homology scheme for aboral-cup-plate circlets. Based on these homologies and a temporal stepwise approach, he used parsimony-based character analyses to develop a subclass-level, phylogenetic classification of the Crinoidea using Arenig and Llanvirn crinoids (Ausich, 1998a). Six subclasses were recognized: Aethocrinea, Cladida, Flexibilia, Articulata, Camerata, and Disparida. The phylogenetic trees generated by Ausich (1998a) confirm many aspects of the Moore and Teichert (1978) classification within subclasses but also indicate that several revisions are necessary, as suggested by Brower (1975), Kelly, Frest, and Strimple (1978), Kelly (1982, 1986), Donovan (1988a), Sevastopulo and Lane (1988), Simms and Sevastopulo (1993), and others.

Developed herein is a comprehensive phylogeny of Arenig to Caradoc crinoids by a continuation of this stepwise approach. This time interval includes the first substantial adaptive radiation of the Crinoidea (Eckert, 1988). During the Arenig and Llanvirn 18 and 16 genera and 19 and 23 species existed, respectively; but during the Caradoc, 76 crinoid genera were present with 259 species recognized. Immediately thereafter, crinoids were diminished in diversity during Ashgillian extinctions (Eckert, 1988; Donovan, 1988a, 1989a, 1994). Based on this phylogeny, a supra-generic classification of Arenig to Caradoc crinoids is presented herein.

The starting point of the current study is the topology of the crinoid phylogeny and subclasses of Ausich (1998a) (Fig. 1), which are based on the homologies of Ausich (1996a). These new homologies are used herein; however, the within-subclass analyses presented here are largely independent of the homology contrasts of Ausich (1996a), except perhaps for the disparids. Furthermore, this work is independent of alternative ideas on the origin of the Crinoidea (Ausich and Babcock, 1998; Ausich, 1998b), except perhaps for the Camerata.

As discussed by Ausich (1997, 1998a), the *Treatise* crinoid classification (Moore and Teichert, 1978) (see Table 1, p. 16) was largely based on work by Moore and Laudon (1943). The Moore and Laudon (1943) classification was largely derived from the competing classification schemes of Wachsmuth and Springer (1897) and Bather (1899, 1900), from a time when very little was known about Early and middle Ordovician crinoids. Therefore, underlying assumptions structuring much of the *Treatise* classification were based largely on Silurian to Mississippian crinoids. This yielded a classification in which the phylogenetic underpinning can be questioned, and, indeed, this is probably the reason for many of the proposed revisions to the *Treatise* classification (see discussions by Ausich, 1997, 1998a).

Due to new and competing ideas on aboral-cup-plate homologies, the origin of crinoids, and what is and what is not a crinoid, phylogenetic and classification analyses herein are built on many assumptions. Assumptions that most or all crinoid students support include elimination of the hemistreptocrinids and coronates from the Crinoidea (Arendt and Rozhnov, 1995; Brett *et al.*, 1983) and dissolution of the subclass Inadunata due to polyphyly (Simms and Sevastopulo, 1993, and others). Assumptions included herein that are probably not endorsed by all crinoid students are: 1. elimination of *Echmatocrinus* from the Crinoidea (Conway Morris, 1993; Ausich and Babcock, 1996, 1998; but see Sprinkle and Collins, 1995); 2. use of rhombiferans as the outgroup for the Crinoidea (Ausich, 1996b, 1998b; but see Guensburg and Sprinkle, 1997, and Sprinkle and Guensburg, 1997); 3. use of the cup-circlet-plate homology scheme of Ausich (1996a); and 4. four-circlet aboral-cup-plate condition as the primitive condition among the Crinoidea (Ausich 1996a, 1996b, 1998a).

METHODS

The methods employed follow Ausich (1998a), who used a progressive, stepwise development of crinoid phylogeny. This method reduces the impact of convergent and iterative evolution among major crinoid clades. The topology of the initial steps of this approach (Arenig to Llanvirn crinoids from Ausich, 1998a) is accepted; and the phylogeny within each of those previously defined clades is examined herein for Arenig to Caradoc forms. Thus, cladids-flexibles, camerates, and disparids of the Arenig to Caradoc are examined independently with parsimony techniques. Furthermore, where necessary, lineage subsets of these clades were also examined. For example, analysis of all camerates yields an overall rather poorly constrained cladogram, but it clearly delineates monobathrid and diplobathrid camerates. Therefore, monobathrids and diplobathrids are analyzed independently further (see discussion of camerates below).

Parsimony-based character analyses are performed using PAUP 3.1.1 (Swofford, 1993). All crinoid stratigraphic information was correlated to the revised Ordovician stratigraphy of Fortey *et al.* (1995). No morphological evidence suggests that the recorded stratigraphic distributions could not be considered accurate at the stage level. No temporal distinctions are made within a stage, however.

For analyses presented herein, all characters are unordered and equally weighted, and all searches were run with 10 random-addition-sequence replicates, with one exception as noted. Search methods used are heuristic with random stepwise addition. Search results are presented as 50-percent majority-rule trees or as single trees. Simple consistency indices (CI), retention indices (RI), and rescaled consistency indices (RC) are given, as indicated in output from PAUP analyses. Specific details for each cladogram are presented below.

Cladograms list generic names, but characters for each genus were typically based on a single species in that genus. Most Tremadoc to Llanvirn genera are monospecific, but most of the Caradoc genera contain many species. The type species was used for character coding where appropriate or necessary. Where more than one species occurs in a genus, the oldest well-preserved species or the type species is used, unless it is poorly known (Appendix A, p. 33). Wherever possible, type specimens or casts of type specimens were examined, including material from Estonia and Russia.

An exhaustive list of morphological characters is not used because the distribution of species-level type characters is likely to add noise to an analysis seeking to uncover the underlying structure of a phylogeny. When a character set is less than comprehensive, however, biases may become a factor. Unfortunately, this is unavoidable. Character selection included those considered to represent basic architectural features of the arms, calyx, and column. Thus, 21 characters were used for cladids and the flexible; 27

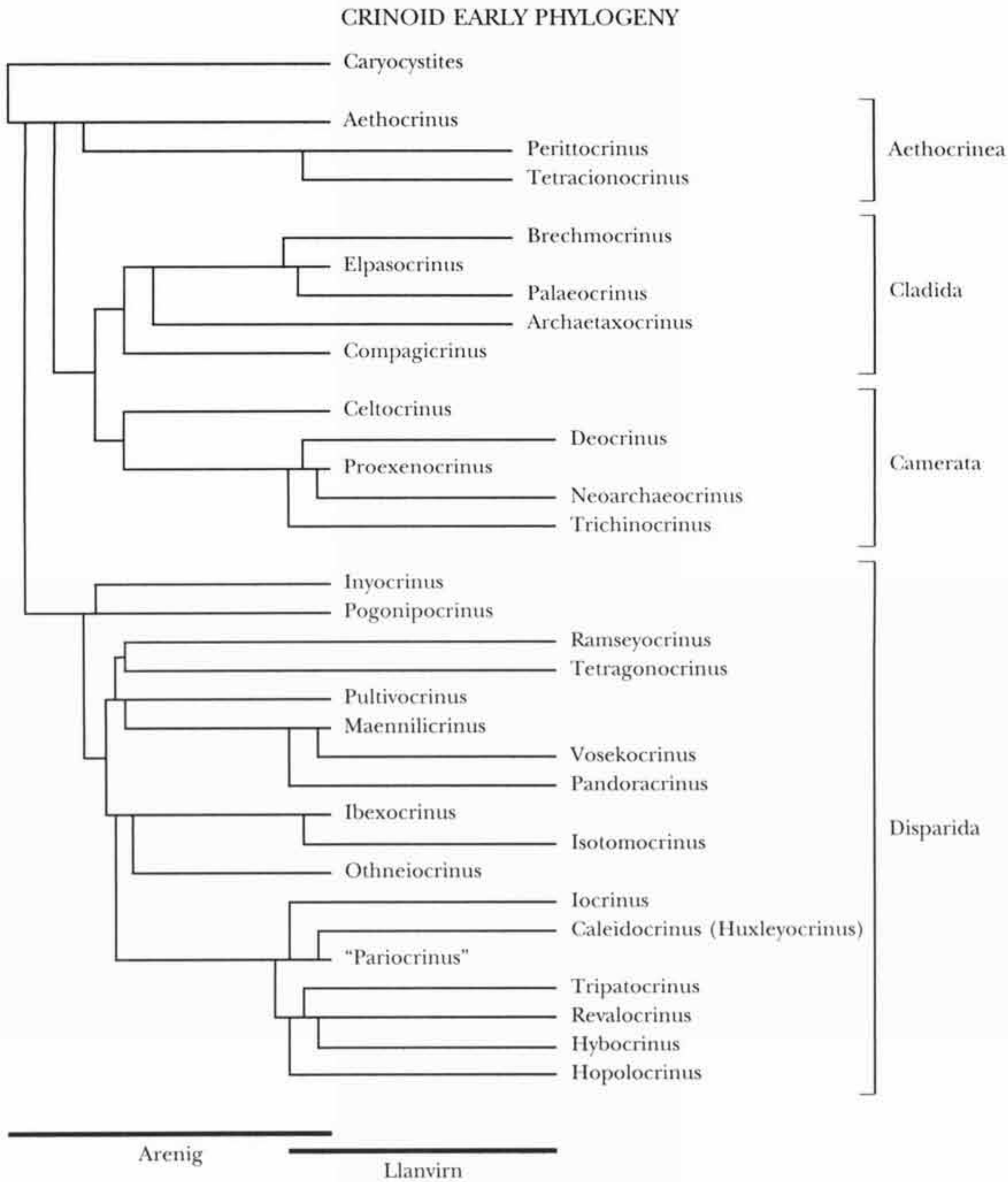


Figure 1. Phylogenetic interpretation of Arenig and Llanvirn crinoids; *Caryocystites* is the outgroup (Ausich, 1998a).

characters were used for camerates; and 31 characters were used for disparids. Some characters were eliminated during preliminary analyses because they were uninformative or because character states could be determined for too few taxa due to limitations of preservation. Examples include the following: cladids—CD interray plating, anal-sac shape, and anal sac-plate sculpturing; camerates—visibility of infrabasals and characters of tegmen; disparids—relative size of C radial, aboral cup-plate sculpturing, and anal-sac shape.

Results of all character analyses and consideration of stratigraphic position, paleogeography, and crinoid morphology were used to develop a final phylogenetic tree for each clade. Stratocladistic methodology (Fisher, 1988, 1994; Harvey and Ausich, 1997) is not used here because in the relatively short interval considered little stratigraphic debt can be reliably accumulated.

Results from character analyses of cladid and flexible crinoids are presented in Figures 2 and 3. In Figure 2, *Elpasocrinus* is the outgroup, and all Arenig to Caradoc cladids are used (22 genera, except *Esthonocrinus, Polycrinus,* and *Triboloporus,* which are poorly known). The analysis included 21 characters (Appendix B, p. 34) with a total of 67 character states. The 50-percent majority-rule tree is

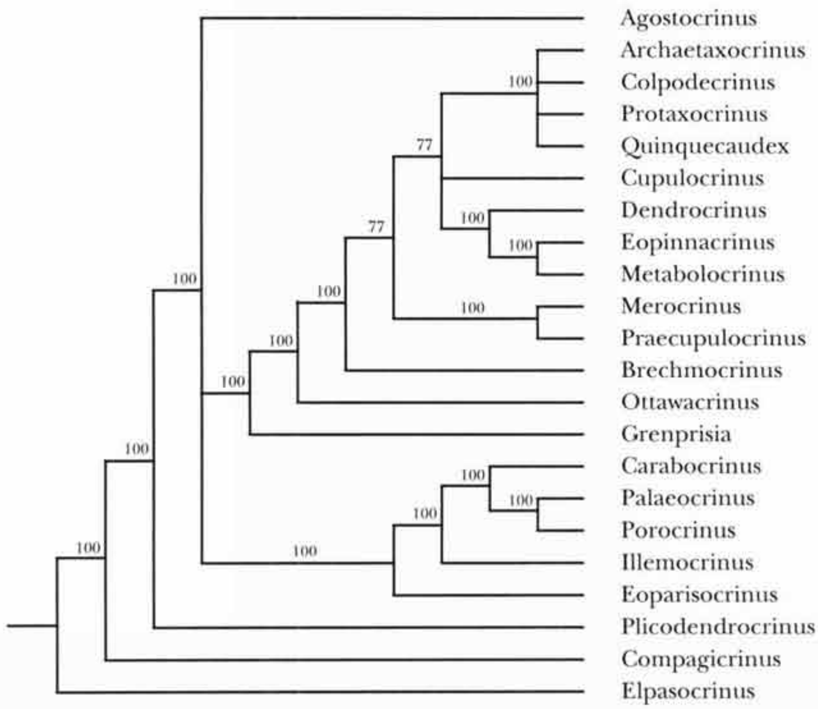


Figure 2. Cladogram from character analysis of all Arenig to Caradoc cladids (22 genera). *Elpasocrinus* is the outgroup. The analysis included 21 characters with a total of 67 character states. The 50-percent majority-rule tree is from 13 equally parsimonious trees; length 76; CI 0.651, RI 0.552, RC 0.360; see also Appendix B, p. 34 (new).

from 13 equally parsimonious trees of length 86, and the tree has a CI = 0.651, RI = 0.552, and RC = 0.360. In Figure 3.1 *Elpasocrinus* is the outgroup, and only dendrocrinid cladids are considered (16 genera). The analysis included 18 characters (Appendix B, p. 34; basal concavity, arm number, and arm habit are constant) with a total of 54 character states. The 50-percent majority-rule tree is from 13 equally parsimonious trees of length 56, and the tree has a CI = 0.714, RI = 0.600, and RC = 0.429. In Figure 3.2, *Elpasocrinus* is the outgroup, and only select dendrocrinids are considered (13 genera). The analysis included 14 characters (Appendix B, p. 34; basal concavity, pore rhombs, arm number, and arm habit are constant) with a total of 47 character states. The 50-percent majority-rule tree is from 8 equally parsimonious trees of length 44, and the tree has a CI = 0.75, RI = 0.560, and RC = 0.420.

Results from character analyses of camerates are presented in Figures 4 and 5. In Figure 4.1, *Proexenocrinus* is the outgroup, and all Arenig to Caradoc camerates are used (26 genera, except *Schizocrinus*). The analysis included 27 characters (Appendix C, p. 35) with a total of 95 character states. The 50-percent majority-rule tree is from 1,021 equally parsimonious trees of length 134, and the tree has a CI = 0.530, RI = 0.537, and RC = 0.284. In Figure 4.2 *Proexenocrinus* is the outgroup for analysis of all monobathrid camerates. Six monobathrids were analyzed, with the exception of *Schizocrinus,* which is poorly known. The analysis included 18 characters (Appendix C, p. 35; ray ridges, extra CD plating, plate size of interray plating, lateral contacts of first primibrachial, regular interray plating, free-arm character, primibrachial number, column construction, and column shape are constant) with a total of 44 character states. The 50-percent majority-rule tree is from 2 equally parsimonious trees of length 27, and the tree has a CI = 0.963, RI = 0.875, and RC = 0.843. In Figure 5.1, *Proexenocrinus* is the outgroup, with all diplobathrids considered (20 genera). The analysis included 25 characters (Appendix C, p. 35; basal number and infrabasal number are constant) with a total of 85 character states. The 50-percent majority-rule tree is from 393 equally parsimonious trees of length 108, and the tree has a CI = 0.562, RI = 0.484, and RC = 0.272. In Figure 5.2, *Proexenocrinus* is the outgroup, and all diplobathrids (except *Euptychocrinus* and *Rhaphanocrinus*) are considered (18 genera). The analysis included 24 characters (Appendix C, p. 35; basal number, infrabasal number, and radial circlet interrupted are constant) with a total of 83 character states. The 50-percent majority-rule tree is from 3 equally parsimonious trees of length 103, and the tree has a CI = 0.592, RI = 0.506, and RC = 0.300.

Results from character analyses of disparids are presented in Figures 6 and 7. In Figure 6, *Pogonipocrinus* is the outgroup, and all Arenig to Caradoc disparids are used (45 genera). The analysis included 31 characters (Appendix D, p. 36; small C radial, plate sculpturing, and anal structure were excluded; interradial plating was constant) with a total of 108 character states. The 50-percent majority-rule tree is from 2,027 equally parsimonious trees of length

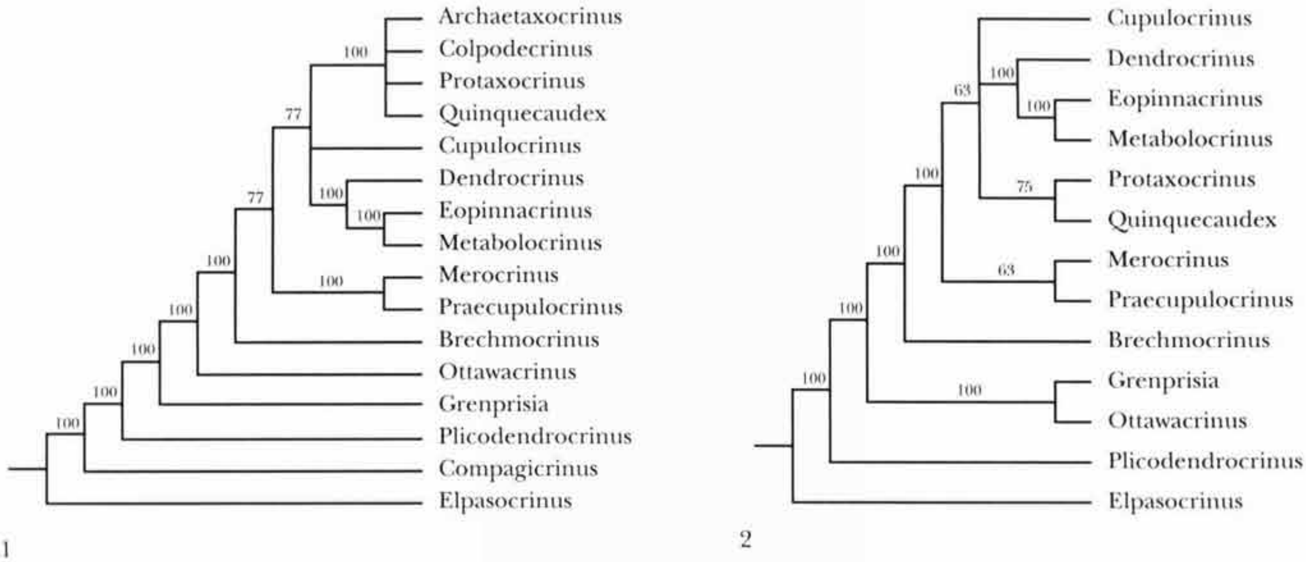


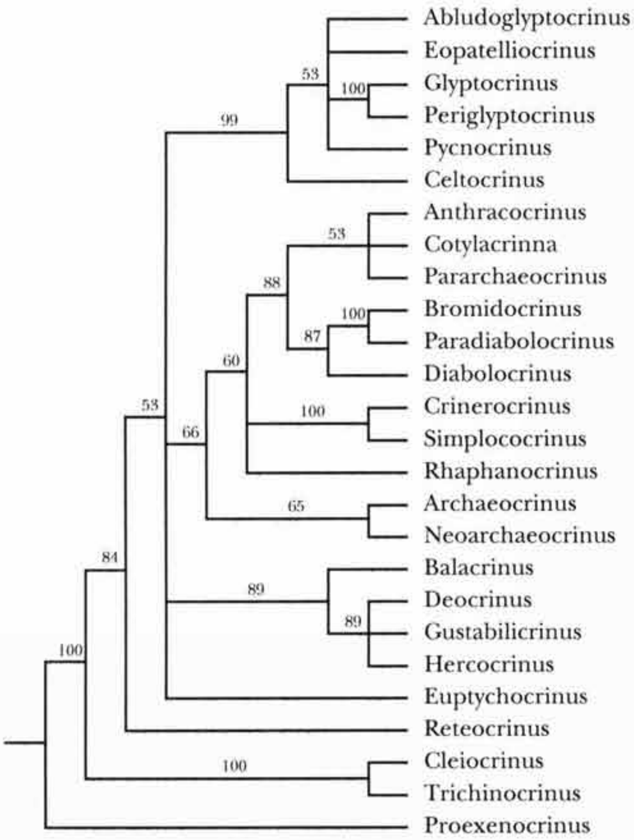
Figure 3. Cladograms from character analysis of select dendrocrine cladids. *1,* Only dendrocrinid cladids considered (16 genera). *Elpasocrinus* is the outgroup. The analysis included 18 characters with a total of 54 character states. The 50-percent majority-rule tree is from 13 equally parsimonious trees; length 56; CI 0.714, RI 0.600, RC 0.429. *2,* Only select dendrocrinids are considered (13 genera). *Elpasocrinus* is the outgroup. The analysis included 14 characters with a total of 47 character states. The 50-percent majority-rule tree is from 8 equally parsimonious trees; length 44; CI 0.750, RI 0.560, RC 0.420; see also Appendix B, p. 34 (new).

210, and the tree has a CI = 0.505, RI = 0.623, and RC = 0.315. The analysis is a single run and not from 10 replicates. In Figure 7.1 *Ibexocrinus* is the outgroup for analysis of homocrinid and cincinnaticrinid disparids, *sensu* Warn and Strimple, 1977 (15 genera, with the exception of *Difficilicrinus, Glaucocrinus,* and *Othneiocrinus*). The analysis included 17 characters (Appendix D, p. 36; A radial, C radial, D radial, E radial, radial-basal articulation, infrabasal number, lintel number, basal concavity, lintels visible, CD plating, interray plating, pore rhombs, arm number, arm habit, recumbent arms, and anal on D ray are constant) with a total of 49 character states. The 50-percent majority-rule tree is from 8 equally parsimonious trees of length 61, and the tree has a CI = 0.721, RI = 0.595, and RC = 0.429. In Figure 7.2, "*Pariocrinus*" (see Systematic Paleontology, p. 27) is the outgroup, and only iocrinid and hybocrinid disparids are considered (12 genera). The analysis included 22 characters (Appendix D, p. 36; A radial, B radial, C radial, D radial, E radial, radial-basal articulation, infrabasal number, basal concavity, interray plating, pore rhombs, and fixed brachials are constant) with a total of 66 character states. A single tree resulted with a length of 57, and the tree had a CI = 0.860, RI = 0.818, and RC = 0.703.

CLADID-FLEXIBLE PHYLOGENY

Character analyses.—Twenty-five genera of Arenig to Caradoc cladids and one flexible are recognized. Of these, three, *Elpasocrinus, Compagicrinus,* and *Archaetaxocrinus,* are known from Arenig strata; *Archaetaxocrinus, Palaeocrinus,* and a new genus (see Systematic Paleontology, p. 18) are from the Llanvirn, and the rest were first recorded from the Caradoc. Three genera, *Esthonocrinus, Polycrinus,* and *Triboloporus,* are poorly known and are not included in any of the character analyses presented below. Details of the analyses are listed above and in the figure captions and appendices.

Inferred phylogeny.—In a comparison of *Elpasocrinus* and *Compagicrinus,* one sees that the posterior interray plating of *Elpasocrinus* is more similar to *Aethocrinus* (see Ausich, 1998a) and later cladids. Therefore, *Elpasocrinus* is taken as the base of the cladid line, having evolved from the aethocrinids through loss of the lintel circlet (Ausich, 1998a). Two cladid lineages arose during the Arenig: *Elpasocrinus* and *Compagicrinus* with the arms free above the radials and no fixed interradials or brachials; and *Archaetaxocrinus,* which had fixed brachials and interradials similar to *Aethocrinus.* In character analysis of all Arenig and Llanvirn crinoids (Ausich, 1998a), *Archaetaxocrinus* falls out as the most derived cladid, intermediate between cladids and camerates. This result is undoubtedly due to the fixed plating at the top of the calyx that is present in both *Archaetaxocrinus* and in camerates. The early age of this form, its retention of basic cladid features, and lack of camerate synapomorphies, however, indicate that it should be retained in the cladids as an early, separate lineage. Lewis (1981) argued that *Archaetaxocrinus* was the oldest flexible crinoid, but this interpretation is incompatible with the present analyses. *Archaetaxocrinus* has features such as fixed brachials and interradials that are similar to flexibles; however, it is considered here to be a cladid lineage distinct from flexibles that added plates in the distal calyx.



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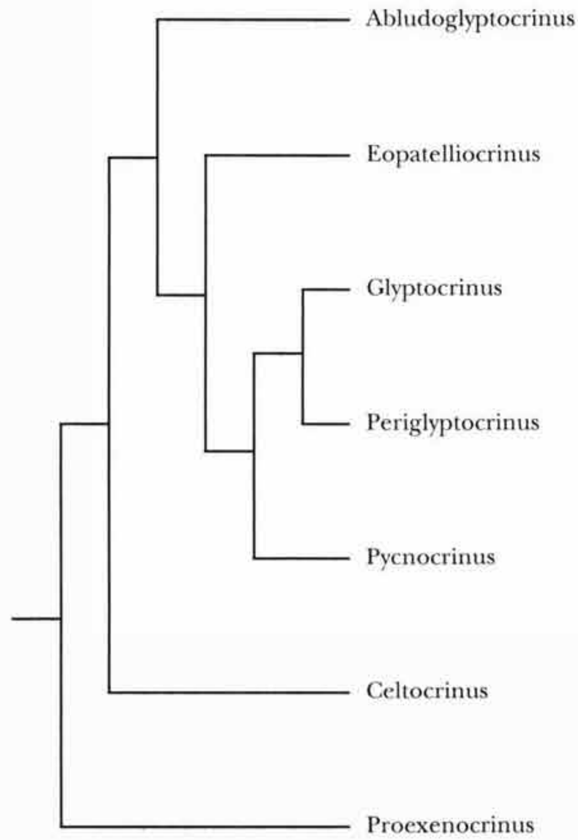

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Figure 4. Cladogram from character analysis of all Arenig to Caradoc camerates. *1,* All Arenig to Caradoc camerates are used (26 genera, except *Schizocrinus*). *Proexenocrinus* is the outgroup. The analysis included 27 characters with a total of 95 character states. The 50-percent majority-rule tree is from 1,021 equally parsimonious trees; length 134; CI 0.530, RI 0.537, RC 0.284. *2, Proexenocrinus* is the outgroup for analysis of all monobathrid camerates. Six monobathrids are analyzed, with the exception of *Schizocrinus*. The analysis included 18 characters with a total of 44 character states. The 50-percent majority-rule tree is from 2 equally parsimonious trees; length 27; CI 0.963, RI 0.875, RC 0.843; see also Appendix C, p. 35 (new).

During the Llanvirn, the cyathocrines became established and persisted through the Caradoc. The three deeply rooted, Arenig to Llanvirn cladid lineages are therefore the dendrocrines, the cyathocrines, and the lineage begun by *Archaetaxocrinus*. Only the dendrocrines and cyathocrines persisted beyond the Caradoc. In addition, dendrocrines and cyathocrines diversified during the Caradoc, and the subclass Flexibilia evolved from the dendrocrines during the Caradoc. Separation between dendrocrines and the derived cyathocrines is evident in the character analysis that includes all cladids and the single flexible (Fig. 2). Cyathocrines became specialized with generally bowl- to globe-shaped aboral cups, narrower radial facets, narrower arms in relation to the aboral cup, and shorter anal sacs. Three early lineages of cyathocrines developed, one lineage with *Eoparisocrinus* and *Illemocrinus,* which are closely related. *Palaeocrinus, Porocrinus, Carabocrinus,* and *Tribolo-porus* constitute the second lineage of cyathocrines and include the conical to globose forms with a well-sutured tegmen, with pore structures, with anus on the tegmen or the side of the cup, and with or without recumbent ambulacra. *Agostocrinus* is a third cyathocrine lineage.

From the Arenig to the Llanvirn, the fundamental dendrocrine lineage comprised *Elpasocrinus, Compagicrinus,* and *Brechmocrinus,* all with compound radianals. This basic lineage continued with the loss of the inferradianal and diversified during the Caradoc to include *Grenprisia, Ottawa-crinus, Plicodendrocrinus,* and *Esthonocrinus.* These crinoids all have medium, cone-shaped, aboral cups; five infrabasals visible in lateral view; high infrabasals; a radianal that occupies the full proximal width of the C radial; angustary to plenary radial facets; mostly three plates in the posterior interray; rounded arms that are either isotomously branched, heterotomously branched, or isotomous proximally and heterotomous distally; and a circular or rarely pentagonal column. From these dendrocrinids a group of crinoids that added fixed plates to the aboral cup includes *Quinquecaudex, Cupulocrinus,* and *Protaxocrinus* (Fig. 3).

A third group of dendrocrines has low to medium, conical, aboral cups; low infrabasals; a radianal that occu-

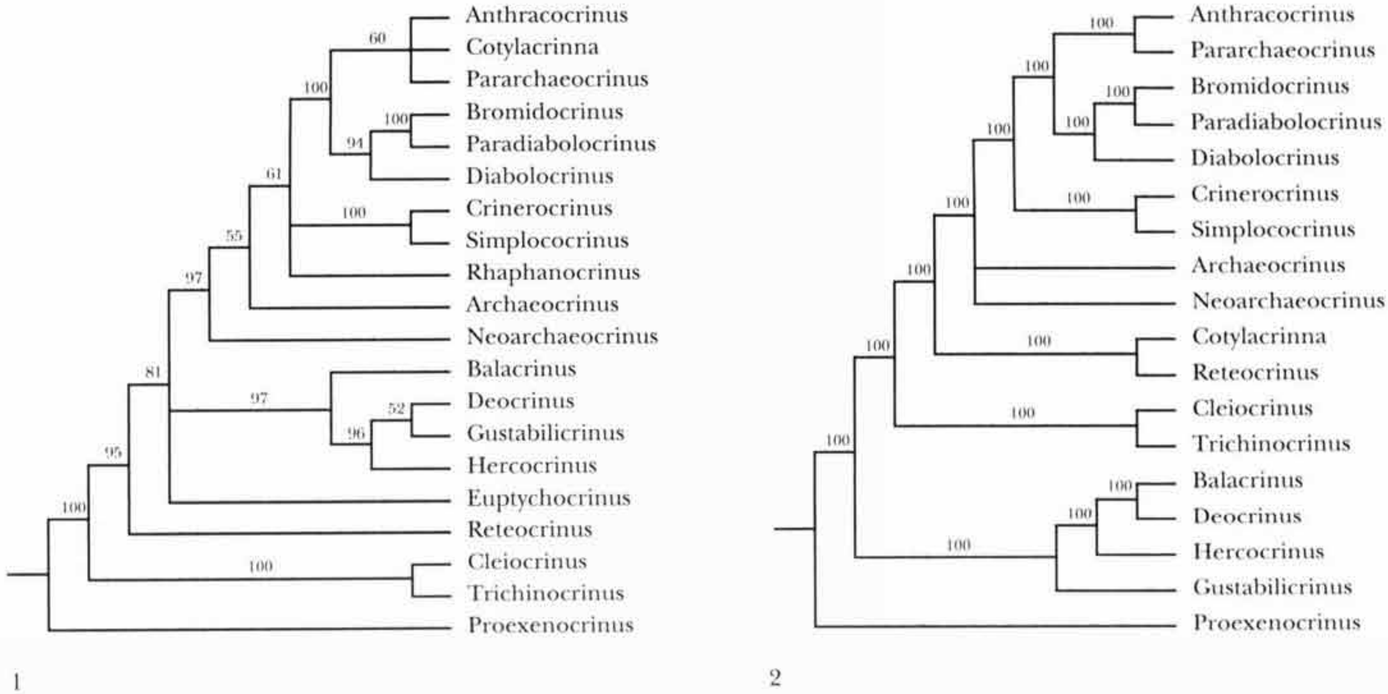

Figure 5. Cladograms from character analysis of select diplobathrid camerates. *1, Proexenocrinus* is the outgroup, with all diplobathrids considered (20 genera). The analysis included 25 characters with a total of 85 character states. The 50-percent majority-rule tree is from 393 equally parsimonious trees; length 108; CI 0.562, RI 0.484, RC 0.272. *2, Proexenocrinus* is the outgroup, and all diplobathrids (except *Euptychocrinus* and *Rhaphanocrinus*) are considered (18 genera). The analysis included 24 characters with a total of 83 character states. The 50-percent majority-rule tree is from 3 equally parsimonious trees; length 103; CI 0.592, RI 0.506, RC 0.300; see also Appendix C, p. 35 (new).

pies the full width of the C radial; peneplenary to plenary radial facets; one to three posterior interray plates in the cup; arms with a wide array of branching modes; and a holomeric, circular column that is either heteromorphic or xenomorphic. Moore, Lane, and Strimple (1978) placed these into numerous families: *Praecupulocrinus* into Cupulocrinidae; *Merocrinus* into Merocrinidae; *Polycrinus* into Mastigocrinidae; "*Dendrocrinus*" *acutidactylus* into Dendrocrinidae (see Systematic Paleontology, p. 21); *Eopinnacrinus* into Botryocrinidae; and *Metabolocrinus* into Metabolocrinidae. These all appear to represent one group of genera modified from the primitive dendrocrinid lineage, however (Fig. 2–3).

In the analysis of all cladids, phylogenetic relationships among *Archaetaxocrinus*, *Colpodecrinus* (see Systematic Paleontology, p. 20), *Protaxocrinus*, and *Quinquecaudex*, all of which have fixed brachials and interradials, are unresolved. *Archaetaxocrinus* and *Colpodecrinus* are regarded as a distinct early cladid branch (Fig. 8) that has fixed brachials and interradials probably as a derived characteristic. *Quinquecaudex* and *Protaxocrinus* evolved from *Cupulocrinus* as a convergent evolutionary trend to increase plates in the calyx. *Cupulocrinus humilis* (Billings) has some individuals with a few small fixed interradial plates. This interpretation of these cladistic results is most consistent with the hypothesis that *Protaxocrinus* is the oldest flexible, as suggested by Springer (1911) and Lane (1978a), and it is recognized as the only Arenig to Caradoc member of the Flexibilia. The essential feature for this transition is the reduction to three infrabasal plates. *Quinquecaudex* is part of the same radiation, but because it retains five infrabasals, it is retained in the cladids.

Another lineage derived from the basic dendrocrinid design was the relatively minor radiation that yielded *Merocrinus, Praecupulocrinus, Polycrinus,* "*Dendrocrinus*" *acutidactylus, Eopinnacrinus,* and *Metabolocrinus* (Fig. 2–3, 8). These crinoids all appear to have arisen as a lineage with medium to low conical cups, very low infrabasals, one radianal, plenary radial facets, one or more primibrachials, and simple to specialized arm branching.

The cyathocrinids are the most derived Arenig to Caradoc cladids. The oldest known cyathocrinid is *Palaeocrinus*, but *Eoparisocrinus* appears to represent a morphology more intermediate between dendrocrinids and cyathocrinids (Fig. 2). *Eoparisocrinus* and *Illemocrinus* represent a more primitive cyathocrinid lineage, whereas the more globular aboral cup design of *Palaeocrinus, Carabocrinus, Porocrinus,* and *Triboloporus*, with reduced arms, pore structures, and recumbent ambulacra, is more specialized in the cyathocrinid lineage. *Agostocrinus* appears to be a cyathocrine crinoid that represents a morphological trend distinct from other Caradoc forms. *Agostocrinus* is

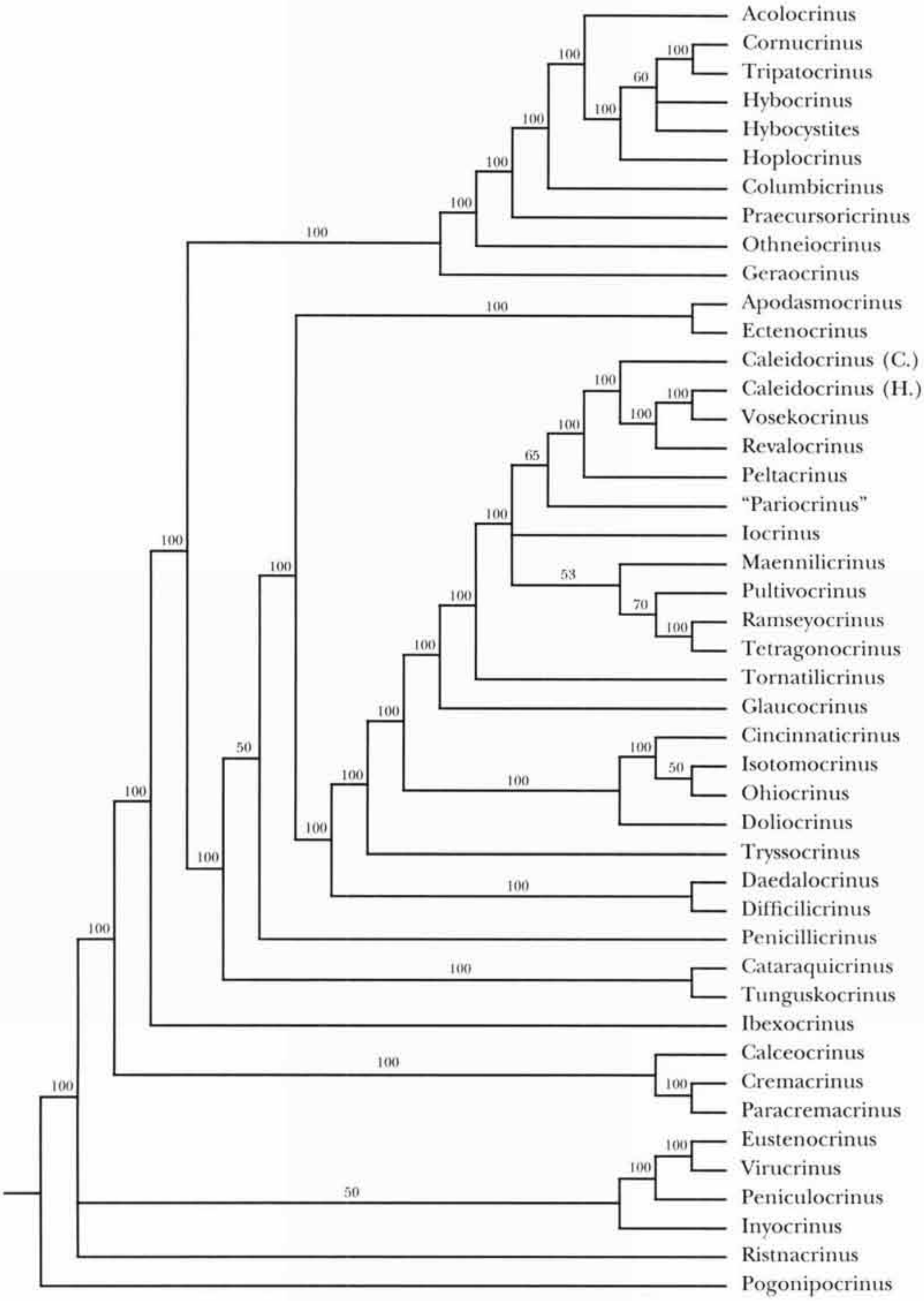

Figure 6. Cladograms from character analysis of all disparid crinoids. *Pogonipocrinus* is the outgroup, and all Arenig to Caradoc disparids are used (45 genera). The analysis included 31 characters with a total of 108 character states. The 50-percent majority-rule tree is from 2,027 equally parsimonious trees; length 210; CI 0.505, RI 0.623, RC 0.315; see also Appendix D, p. 36 (new).

considered a cyathocrine because of the cup shape, well-sutured tegmen plates, and apparent lack of an anal sac. Its recumbent arms and large radianal in the basal circlet make it a separate lineage.

Discussion.—Brower (1995a) analyzed the phylogeny of Ordovician and Early Silurian cladid crinoids on the basis of 42 characters. Methods included cluster analysis and PAUP, and the plate homologies used were essentially the same as those of Moore and Teichert (1978). Cladids were divided into five basic groups (Brower, 1995a) (only Arenig to Caradoc crinoids are listed here): 1. stem cladids *Aethocrinus, Compagicrinus, Elpasocrinus, Grenprisia,* and *Ottawacrinus;* 2. *Carabocrinus, Palaeocrinus, Illemocrinus,* and *Porocrinus;* 3. *Archaetaxocrinus, Merocrinus, Praecupulocrinus,*

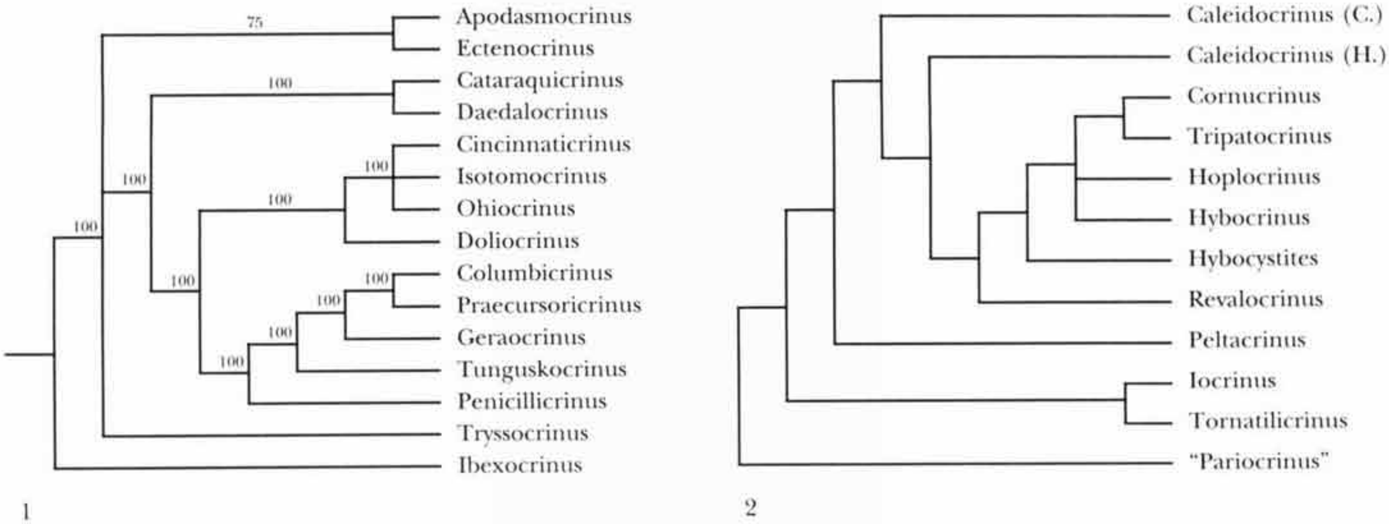

Figure 7. Cladograms from character analysis of select disparid crinoids. *1, Ibexocrinus* is the outgroup for analysis of homocrinids, cincinnaticrinids (*sensu* Warn and Strimple, 1977), and disparids (15 genera, with the exception of *Difficilicrinus, Glaucocrinus*, and *Othneiocrinus*). The analysis included 17 characters with a total of 49 character states. The 50-percent majority-rule tree is from 8 equally parsimonious trees; length 61; CI 0.721, RI 0.595, RC 0.429. *2*, "*Pariocrinus*" is the outgroup, and only iocrinid and hybocrinid disparids are considered (12 genera). The analysis included 22 characters with a total of 66 character states. A single tree resulted with a length of 57; CI 0.860, RI 0.818, RC 0.703; see also Appendix D, p. 36 (new).

and *Polycrinus;* 4. *Cupulocrinus* and *Protaxocrinus;* and 5. *Dendrocrinus, Esthonocrinus, Eoparisocrinus, Eopinnacrinus, Plicodendrocrinus*, and *Quinquecaudex*.

The analyses herein and that of Brower (1995a) agree on many basic groupings of these cladids. They also agree on some potentially contentious issues: 1. *Archaetaxocrinus* is deeply rooted and not related to flexible crinoids; 2. *Ottawacrinus* is a primitive cladid closely related to *Grenprisia;* 3. *Merocrinus, Praecupulocrinus*, and *Polycrinus* are closely related; and 4. *Protaxocrinus* is closely related to *Cupulocrinus*. These two independent analyses disagree on several points, however, including the following: 1. *Eopinnacrinus* was considered to be a dendrocrinid by Brower (1995a) but is regarded herein as a metabolocrinid; 2. *Eoparisocrinus* was considered to be a dendrocrinid by Brower (1995a, 1995b), but it links with other cyathocrines herein; and 3. *Quinquecaudex* was considered to be a dendrocrinid by Brower (1995a) but is considered herein to be a cupulocrinid. The interpretations presented here are preferred because the choice of characters and homologies used are considered to be fundamental to crinoid designs and because the lineages identified here can be organized into well-defined superfamilies and families based on basic aspects of the aboral-cup architecture and arm characteristics (see Systematic Paleontology, p. 19–22).

CAMERATE PHYLOGENY

Character analysis.—Five Arenig to Llanvirn camerates were recognized by Ausich (1998a), with *Celtocrinus* being the only monobathrid (two-circlet) camerate and *Proexenocrinus* being the oldest and most primitive diplobathrid (three-circlet camerate). Twenty-seven Arenig to Caradoc camerates are known (Appendix C, p. 35). Relationships among these crinoids are delineated with four character analyses (Fig. 4–5): all camerates, only monobathrids, and only diplobathrids (two analyses). For camerates, all Arenig to Caradoc camerates are analyzed with the exception of *Schizocrinus* Hall, which is very poorly known. Details of the analyses are provided above and in the figure captions and appendices.

Inferred phylogeny.—As discussed by Ausich (1998a), the early camerates are phylogenetically close to early dendrocrinid cladids, with cladids being more primitive. Cladograms from character analyses of these early crinoids have cladids and camerates ladderized (Ausich, 1998a), with key camerate characters (although not maintained by all taxa) being the incorporation of fixed brachials and interradials, pinnulate arms, and change in the posterior interray (Ausich, 1998a). Both three- and two-circlet camerates occur at the start of the Arenig with *Proexenocrinus* and *Celtocrinus*, respectively. Verified both by character analyses of all camerates (Fig. 4.1) and of monobathrids only (Fig. 4.2), *Celtocrinus* is linked with other monobathrids and should be regarded as the base of this monophyletic clade. Similarly, *Proexenocrinus* is considered to be the base of the diplobathrid clade (Ausich, 1998a).

Proexenocrinus is a simple diplobathrid, with relatively few fixed brachials and interradials, ten nonbranching arms with uniserial pinnulation, and first interradials and basals in contact in all interrays, thus separating all radial plates (Ausich, 1986b). This condition, the rhodocrinitacean arrangement, is present in all Arenig to Caradoc diplobathrids except *Euptychocrinus*.

From *Proexenocrinus* six diplobathrid lineages became established during the Llanvirn. The first was a continuation of the basic morphology of *Proexenocrinus* to yield the

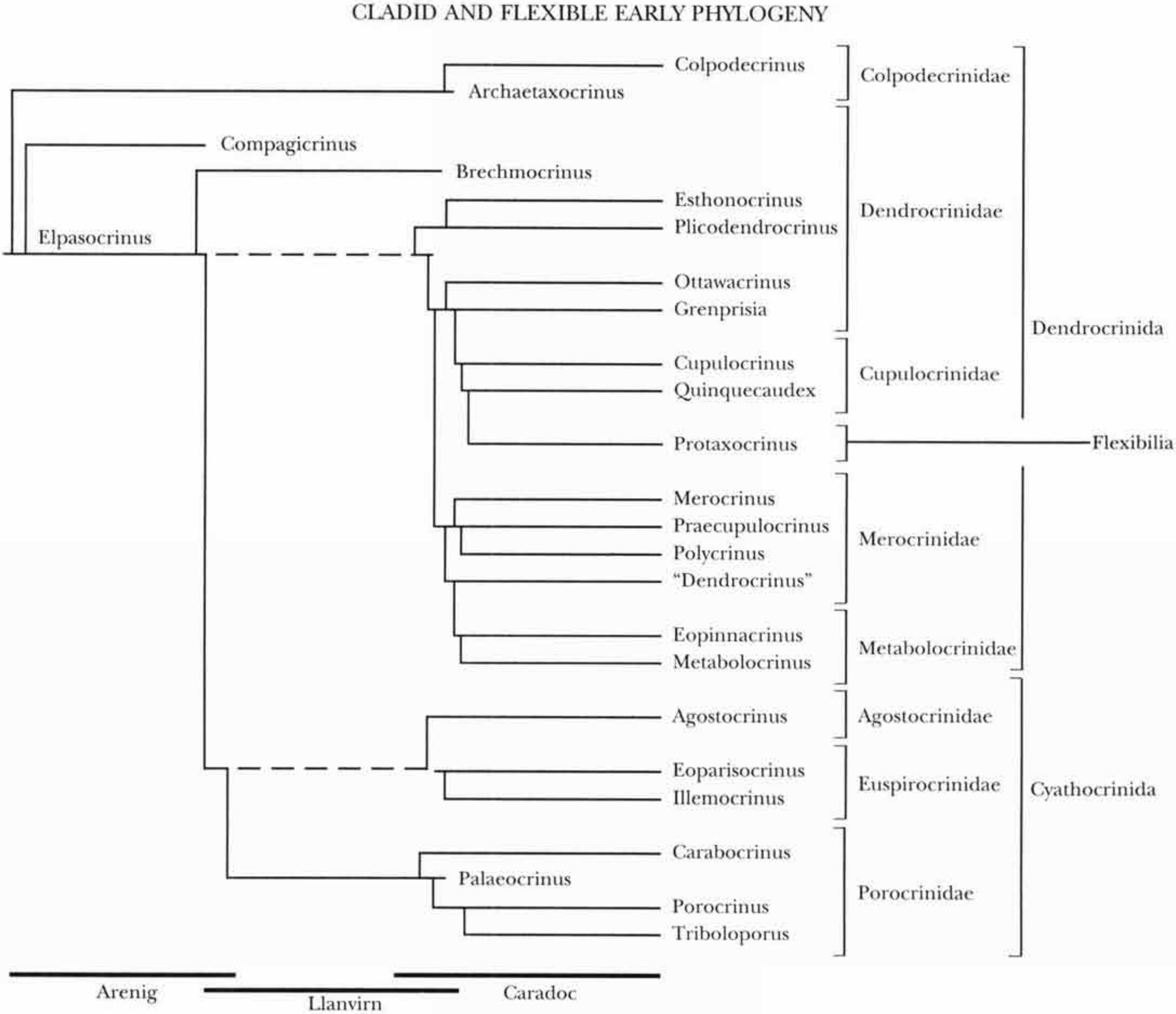

Figure 8. Phylogenetic interpretation of cladid crinoids with one flexible, *Protaxocrinus*, included (new).

Archaeocrinidae-Rhodocrinitidae of Ubaghs (1978c). This lineage was the principal Caradoc diplobathrid radiation. *Euptychocrinus* and *Reteocrinus* are two unusual Caradoc diplobathrids that are consistently linked peripherally to other diplobathrids in cladograms herein (Fig. 4.1, 5.1). Both were probably derived from *Neoarchaeocrinus* or a similar form, and each was an independent lineage (Fig. 9). As mentioned above, *Euptychocrinus* represented a change to an architecture with the radial circlet complete, except for the posterior interray. Whereas this is a unique Arenig to Caradoc diplobathrid morphology, it records the base of the dimerocrinitaceans that diversified during the Silurian. *Reteocrinus* is also a very unusual Arenig to Caradoc diplobathrid because it has very small, irregular interradial plating; no large first interradial plate; and no pinnules. This is a lineage that did not persist beyond the Ordovician.

Trichinocrinus, the fourth lineage, is another unusual diplobathrid because its posterior interray is similar to the cladid posterior interray (Ausich, Bolton, and Cumming, 1998) and may be a reversal to that condition. *Trichinocrinus* has an asymmetrical posterior interray with a single large plate in sutural contact with the CD basal. The anitaxis and anitaxial ridge are derived from a heptagonal C radial. The essential features of this unusual posterior interray also occur in *Pararchaeocrinus* (see Kolata, 1982), but these two forms are otherwise similar to other archaeocrinids-rhodocrinitids. In contrast, in other camerates, the posterior interray is bilaterally symmetrical, and it begins on a single plate, the primanal, at the proximal part of the interray. Typically either two or three plates form the first range of plates above the primanal, and if an anitaxis and or anitaxial ridge is present its origin is from the primanal.

A fifth lineage comprises only *Cleiocrinus*. *Cleiocrinus* consistently links with *Trichinocrinus* in parsimony analyses (Fig. 4.1, 5), but this probably reflects that these two forms are significantly different from other diplobathrids rather than the fact that they are similar to one another. *Cleiocrinus* is linked to *Trichinocrinus* in analyses herein because both have a simple, small aboral cup with a basal concavity, no fixed pinnules, cuneate uniserial arms, no intrabrachials, and atomous free arms. *Cleiocrinus,* however, is so unusual that its origin from other diplobathrids is problematic. Whereas *Cleiocrinus* has a small aboral cup, it has a huge calyx composed of hypertrophied, fused brachials. Small pores penetrate the calyx at triple junctions among fused brachials, no intrabrachials are present, and the posterior interray is composed exclusively of the anitaxis. For the present, this unique Ordovician crinoid is regarded questionably as having been derived from *Proexenocrinus,* but no intermediate forms are known, and no Llanvirn ancestor is known. It is improbable that *Cleiocrinus* was derived from *Trichinocrinus,* because it lacks the synapomorphies of *Trichinocrinus* and *Pararchaeocrinus.*

The sixth diplobathrid lineage from *Proexenocrinus* was established from *Deocrinus* and also includes *Hercocrinus, Gustabilicrinus,* and *Anthracocrinus;* these are the Anthracocrinidae of Ubaghs (1978c). This lineage did not survive beyond the Caradoc.

Despite the lack of a Llanvirn monobathrid, *Celtocrinus* is certainly the root of the monobathrid clade because it has the basic characteristics of the Glyptocrinidae, which, with the exception of *Eopatelliocrinus,* represents the Arenig to Caradoc radiation of monobathrids (Fig. 4.1, 5.2, 9). *Abludoglyptocrinus* is apparently the most primitive Caradoc glyptocrinid (Fig. 4.2). *Eopatelliocrinus* is inferred to have evolved from *Abludoglyptocrinus.* Unlike glyptocrinids with a large calyx composed of several fixed brachials and interradials, *Eopatelliocrinus* has a much simplified calyx with very few fixed brachials and interradials (Brower, 1994). This began the patelliocrinacean lineage.

Discussion.—Early phylogeny of camerates was confused by Ubaghs (1978b) because *Proexenocrinus* was considered at that time to be a monobathrid (see Ausich, 1986b). Ubaghs (1978b) indefinitely linked major groups, although he did regard archaeocrinids as the stock from which other diplobathrids arose. This is consistent with the interpretation herein and with the interpretation of *Proexenocrinus* as a diplobathrid. Origins of monobathrids were problematic to Ubaghs (1978b), again due in part to *Proexenocrinus.* An intermediate form between diplobathrids and monobathrids (Ubaghs, 1978b), however, has still not been found.

Origins and relationships among camerates presented here differ substantially from those proposed by Donovan (1988a) and Simms (1994a, 1994b). Donovan (1988a) used *Echmatocrinus* as the outgroup for crinoids (see Ausich and Babcock, 1996, 1998), which led to a different topology; and Simms (1994b) used very different plate-circlet homologies.

DISPARID PHYLOGENY

Character analysis.—Among the earliest crinoids, the Disparida are the most diverse, with 45 genera considered here. The disparids are an interesting combination of mostly conservative, relatively simple forms with few, very distinctive, derived types. This combination is not well suited for robust parsimony character analysis. The advantages of a stepwise approach to parsimony character analysis is most evident among the disparids. Analysis of all genera (Fig. 6) is poorly resolved and cannot be interpreted clearly. Disparid phylogeny, however, can be understood from consideration first of relationships among Arenig and Llanvirn disparids (Ausich, 1998a) and then by adding analyses of Caradoc forms. Analyses of various subsets of the disparids are required to understand detailed relationships. Details of the analyses are listed above and in the figure captions and appendices.

Inferred phylogeny.—The initial disparids evolved through loss of the basal circlet from the four-circlet aethocrinid condition with five plates in each circlet (plus the posterior plates; Ausich, 1998a). Therefore, the most primitive disparid had five lintels, five infrabasals, and five radials, such as *Pogonipocrinus* (see Kelly and Ausich, 1978, 1979) and *Inyocrinus* (see Ausich, 1986b). The basic topology of disparid phylogeny was established during the Arenig and Llanvirn (Fig. 1). In this earliest radiation, six additional fundamental lineages became established that are identifiable on the pattern of loss of radial plates and architecture of the aboral cup. These lineages are treated here at the ordinal rank. One additional order, Calceocrinida, became established during the Caradoc. Lineages that became established include: 1. those with five infrabasals and five radials; 2. the lineage beginning with *Pultivocrinus* that lost all radials; 3. the lineage beginning with "*Pariocrinus*" that retained a single radial plate in the C ray; 4. the highly specialized hybocrinids that also retained only the C radial; 5. the homocrinid-cincinnaticrinid lineage that began with *Ibexocrinus* with genera losing various radial plates; and 6. *Ramseyocrinus* and *Tetragonocrinus* that lost all plates in the cup except the lintels (Fig. 1). The calceocrinids were the seventh lineage, and these unique crinoids first appeared during the Caradoc. These seven basic clades are evident on the cladogram that includes all disparids (Fig. 6). This character analysis, although not particularly robust, still has most branches with 100-percent agreement and also identifies several key relationships, including the following: 1. crinoids with five (or four) infrabasals and five (or four) radials are grouped adjacent to the outgroup on a basal polytomy

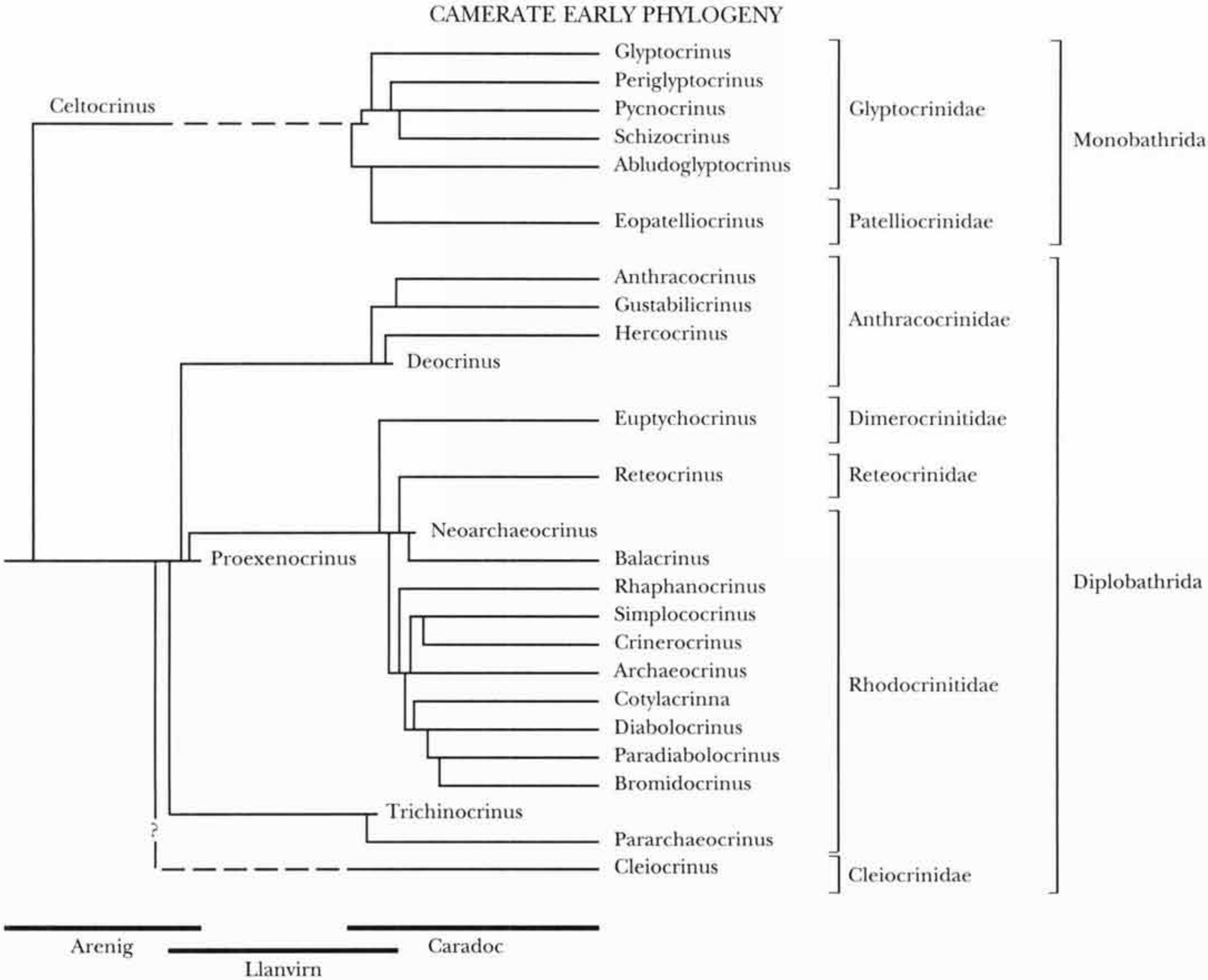

Figure 9. Phylogenetic interpretation of camerate crinoids (new).

(*Pogonipocrinus, Ristnacrinus, Inyocrinus, Peniculocrinus, Eustenocrinus,* and *Virucrinus*); 2. *Ramseyocrinus* and *Tetragonocrinus* are linked; 3. *Ibexocrinus* is deeply rooted (an early branch) in the tree; and 4. even in parts of the cladogram that are poorly resolved, crinoids with one radial plate and those without radial plates are each fairly well linked (Fig. 6).

Figures 10 and 11 illustrate the inferred relationships among Arenig to Caradoc disparids. No Llanvirn disparids are known with both infrabasals and radials in every ray. It is reasonable, however, to assume that the Arenig and Caradoc crinoids with this morphology are closely related. Two unusual genera in this clade are *Virucrinus,* which lost one ray, so that it has four infrabasals and four radials, and *Acolocrinus,* which developed three lintels, radial processes, multiple armlets on radial facets, and pore structures. *Ristnacrinus* is considered to be the most primitive Caradoc form in this clade.

The extremely paedomorphic *Ramseyocrinus* and *Tetragonocrinus* had a cup composed of a single circlet, the lintels, and left no descendants after the Llanvirn. This new interpretation of these unusual crinoids agrees, in part, with Donovan (1988b, 1989b) and Rozhnov (1988, 1989), who independently argued that *Ramseyocrinus* and *Tetragonocrinus* had an aboral cup composed of a single circlet of plates: *Ramseyocrinus* with the radial circlet (Donovan, 1989b) and *Tetragonocrinus* with the infrabasal circlet (Rozhnov, 1988, 1989). The interpretation of the homology of this plate with the lintels of *Aethocrinus* is new, however.

Those disparids that lost all radials but retained all infrabasals did not survive into the Caradoc either. These include *Pultivocrinus* and *Maennilicrinus* from the Arenig and *Vosekocrinus* and *Pandoracrinus* from the Llanvirn. *Maennilicrinus* is inferred to be the ancestor of these Llanvirn forms (Fig. 10).

Various additional character analyses were also performed on the rest of the disparids in order to develop a more robust understanding of these relationships; two are presented here (Fig. 7). Figure 7.1 includes Llanvirn and Caradoc disparids that lost two to four radial plates, including those placed by Moore *et al.* (1978) in the Homocrinacea and in the Heterocrinacea (=Cincinnaticrinacea of Warn and Strimple, 1977). This character analysis yields eight equally parsimonious trees. The resultant concensus-tree cladogram cannot be taken as the phylogenetic tree for these crinoids because one polytomy exists and because *Isotomocrinus* should presumably be more deeply rooted as it occurs in Llanvirn strata. This Caradoc radiation occurred entirely in North America, with the exception of *Tunguskocrinus* from the Siberian Platform, Russia. Therefore, despite the similarity of the aboral cup architecture of *Tunguskocrinus* to homocrinids, it is possible that *Tunguskocrinus* represents convergence and is not closely related to other homocrinids. Despite the fact that no Llanvirn homocrinids exist, this analysis and the phylogenetic reconstruction assume that all homocrinids evolved directly through *Ibexocrinus* rather than the homocrinids having been derived from *Isotomocrinus*, which would require first loss, then reevolution of the B radial. *Ectenocrinus* is regarded as the Caradoc homocrinid stock from which all others arose. It is thought to have evolved from *Ibexocrinus* or a similar form. From *Ectenocrinus*, six additional homocrinids arose during the Caradoc. Homocrinid-derived forms that are not shown in Figure 7.1 are the calceocrinids and *Glaucocrinus*. The calceocrinids branch near the base on the cladogram derived from analysis of all disparids (Fig. 6). The calceocrinids *Cremacrinus*, *Calceocrinus*, and *Paracremacrinus* are considered to be a lineage that diverged early and independently from the rest of the homocrinids, as indicated in Figure 6. Harvey and Ausich (1997) recently considered the phylogeny of the calceocrinids, which is given in Figure 11. Despite the fact that Guensburg (1992) did much to clarify the morphology of *Glaucocrinus*, questions about it remain. The sole specimen is poorly preserved, so some aspects of its unusual morphology may be a preservational artifact, or this may simply be an aberrant form. Therefore, it was not used in any analyses.

All character analyses performed on homocrinids-cincinnaticrinids, regardless of the taxa, outgroup, or characters considered, consistently grouped three cincinnaticrinids, *Columbicrinus*, *Praecursoricrinus* (see Systematic Paleontology, p. 27), and *Geraocrinus*, separately from the other cincinnaticrinids, *Cincinnaticrinus*, *Isotomocrinus*, *Doliocrinus*, and *Tryssocrinus*. Two alternative interpretations could explain this pattern: the loss of the B radial, the defining characteristic for the Cincinnaticrinidae (=Heterocrinacea of Moore and Lane, 1978a) may have happened twice, and the character analyses presented in Figures 6 and 7.1 accurately reflect crinoid evolution; or these character analyses are flawed in some way, and the loss of the B radial among these crinoids was a unique evolutionary event. Until additional data suggest otherwise, I favor the former interpretation for three reasons: given available data separation between these taxa is very consistent; loss of radial plates was a changeable character during this early disparid diversification; and other disparids independently lost the B radial, e.g., "*Pariocrinus*" and its descendants, *Maennilicrinus* and its descendants, *Paracremacrinus*, and *Othneiocrinus*.

In summary, disparids that lost between two and four radial plates represent a single adaptive radiation from *Ibexocrinus* with five evolutionary lineages. First, *Othneiocrinus* is an unusual Arenig form that has different radial facet types in different rays and pinnulate arms. It did not give rise to descendants, as far as is known. Second, the basic homocrinid morphology supported the interpretation of a radiation of six additional genera. Third, *Isotomocrinus* became the first of the cincinnaticrinids that also included *Cincinnaticrinus*, *Ohiocrinus*, *Doliocrinus*, and *Tryssocrinus*. The fourth group includes *Columbicrinus*, *Praecursoricrinus*, and *Geraocrinus*. Fifth, the calceocrinids with a hinged aboral cup and bilaterally symmetrical crown developed from the homocrinid stock.

Finally, disparids that retained a single radial plate (C radial) form two distinct clades. The oldest member of this group is "*Pariocrinus*" Rozhnov, 1988 (*non Pariocrinus* Eckert, 1984) (Fig. 1). "*Pariocrinus*" first appeared during the Arenig as the base of the iocrinid clade, and the hybocrinids began to diversify during the Llanvirn. Iocrinids include "*Pariocrinus*," *Iocrinus*, *Tornatilicrinus*, *Peltacrinus*, and *Caleidocrinus* and have cone- or bowl-shaped aboral cups, plenary to peneplenary radial facets, and arms all erect and branching. In contrast, the hybocrinids have a globose aboral cup, may have recumbent ambulacra, and have angustary radial facets; and where erect arms occur they are atomous. A single most parsimonious tree results regardless of whether "*Pariocrinus*," *Iocrinus*, or *Caleidocrinus (Huxleyocrinus)* is used as an outgroup. In all cases, the hybocrinids are linked most closely with *Caleidocrinus (H.)*. "*Pariocrinus*" is stratigraphically the oldest of these crinoids; the cladogram with it as outgroup is shown in Figure 7.2. This group probably began as an early branch from *Ibexocrinus* (Fig. 1, 10) by losing all radials except the C radial. *Revalocrinus* is intermediate between iocrinids and hybocrinids, and its traditional treatment as the oldest hybocrinid (Sprinkle and Moore, 1978) is followed here.

CLASSIFICATION

Introduction.—Results of these phylogenetic studies indicate that many changes are required in the suprageneric classification of Moore and Teichert (1978) (Table 1) if a phylogenetic classification is to be maintained. Unfortunately, these results do not permit a comprehensive classification of the Crinoidea, but they do provide a means

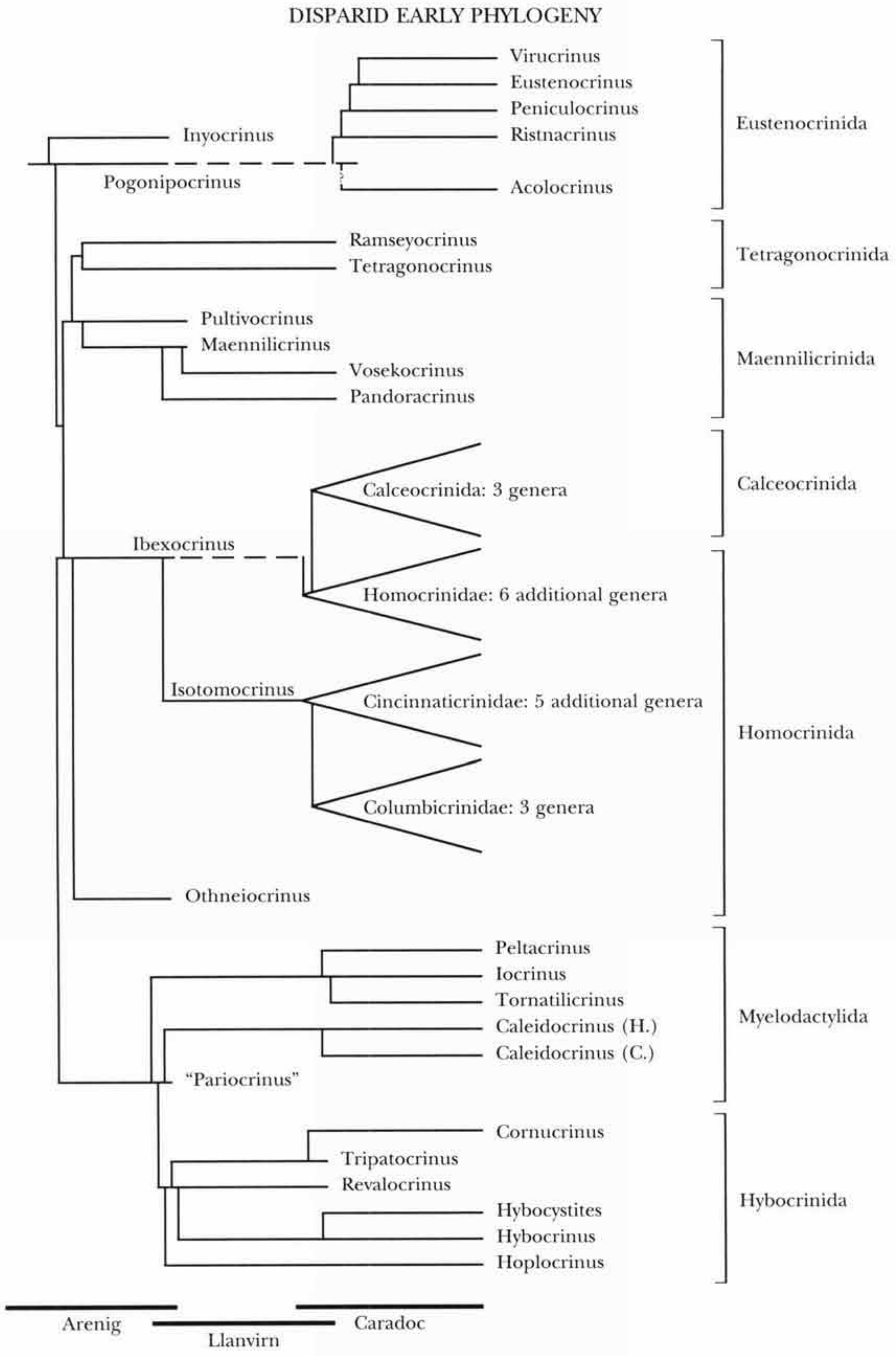

Figure 10. Phylogenetic interpretation of disparid crinoids (new).

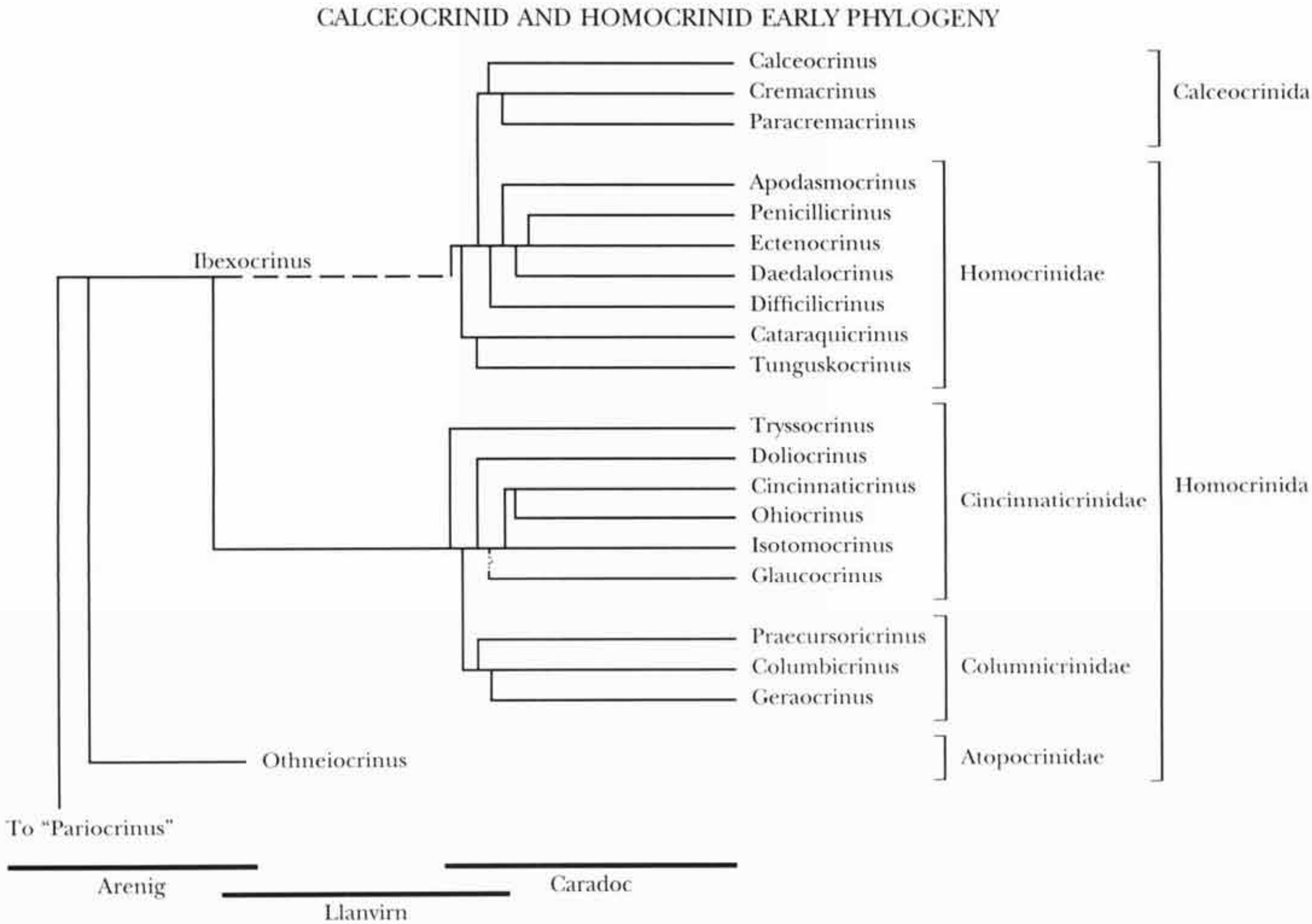

Figure 11. Phylogenetic interpretation of calceocrinid and homocrinid disparid crinoids (new).

to understand the classification of early forms. Completion of a comprehensive classification awaits further phylogenetic analysis of younger crinoids.

As argued by Ausich (1998a) if a hierarchical, Linnaean classification is to be developed, paraphyletic groups must be recognized, as they are herein. The basic topology of crinoid diversification and the grouping of crinoids into subclasses follows Ausich (1998a). This follows the *Treatise* (Moore and Teichert, 1978) (Table 1) with the exceptions that the Inadunata is considered to be polyphyletic, so the Cladida and Disparida are recognized as subclasses (Simms and Sevastopulo, 1993) (Table 2), the coronates are blastozoans (Brett *et al.*, 1983), and the hemistreptocrinids are regarded as columns (Arendt and Rozhonov, 1995).

In the present classification, disparids, camerates, flexibles, and articulates are monophyletic. The aethocrinids and cladids are paraphyletic (Ausich, 1998a). Wherever possible, a conservative approach has been taken regarding the grouping of crinoids into subclasses; i.e., names and ranks given by Moore and Teichert (1978) are maintained. This minimizes the number of new names but does result in classifications within subclasses that are not always parallel. For example, the order Diplobathrida is divided into superfamilies, whereas the order Monobathrida is divided into suborders (Table 3).

Aethocrinida.—The least diverse but most primitive crinoid subclass is the Aethocrinea. As argued by Ausich (1998a), this subclass contains three genera grouped into two families and is included in a single order (Table 3 and in Systematic Paleontology, p. 19). It is regarded as a paraphyletic group that retains the most primitive crinoids.

Cladida.—Cladids are a subclass, as first suggested by Kelly (1982, 1986) and formally designated by Simms and Sevastopulo (1993). Moore, Lane, and Strimple (1978) subdivided the order Cladida into three suborders, the Cyathocrinina, Dendrocrinina, and Poteriocrinina. The validity of these suborders has been questioned by numerous authors (among others, McIntosh, 1986; Sevastopulo and Lane, 1988; Simms and Sevastopulo, 1993). I support recognition of the dendrocrines as the primitive cladids and of the cyathocrines as a derived cladid group (Lane, 1978b). With cladids recognized as a subclass, the

Table 1. Crinoid classification by Moore and Teichert (1978).

- Class Crinoidea
    - Subclass Echmatocrinea
        - Order Echmatocrinida
    - Subclass Camerata
        - Order Diplobathrida
        - Order Monobathrida
    - Subclass Inadunata
        - Order Disparida
        - Order Hybocrinida
        - Order Coronata
        - Order Cladida
    - Subclass Flexibilia
        - Order Taxocrinida
        - Order Sagenocrinida
    - Subclass Articulata
        - Order Millericrinida
        - Order Cyrtocrinida
        - Order Bourgueticrinida
        - Order Isocrinida
        - Order Comatulida
        - Order Uintacrinida
        - Order Roveacrinid
- Class Hemistreptocrinoidea[1]
        - Order Hemistreptocrinida

[1]new class of Crinoidea proposed by Arendt (1976)

Dendrocrinida and Cyathocrinida are elevated to ordinal rank. The relationship of the pinnule-bearing poteriocrines to other cladids is beyond the scope of this study, and this important issue requires additional attention.

The difficult question for unraveling the phylogeny and classification of these early cladids is determining which taxa are morphological experiments that were convergent on later morphologies and did not radiate subsequently, and which were the beginnings of clades that radiated during the Silurian and Devonian. Moore, Lane, and Strimple (1978) and subsequent authors placed Arenig to Caradoc dendrocrines into two superfamilies, the Dendrocrininea and the Merocrininacea. The principal distinction between these superfamilies was that the former has angustary radial facets and the latter has plenary radial facets (Moore, Lane, and Strimple, 1978). New taxa described since 1978 blur this single-character distinction, as genera assigned to each superfamily may have peneplenary radial facets.

The Dendrocrinidae are regarded as the basic stock of cladid crinoids. The four evolutionary departures from this basic lineage are all regarded differently. The Llanvirn experimentation of adding fixed plates above the radial circlet resulted in *Archaetaxocrinus* and questionably *Colpodecrinus*. These two taxa are assigned to the Colpodecrinidae, but this designation is not as strong as others below. The Caradoc experimentation of adding plates yielded two genera assigned to the Cupulocrinidae, *Cupulocrinus* and *Quinquecaudex*. *Protaxocrinus*, the first flexible crinoid, arose from this radiation. The Merocrinacea include a group of dendrocrines that developed much shorter aboral cups with much less conspicuous infrabasals, including *Merocrinus*, *Praecupulocrinus*, *Polycrinus*, "*Dendrocrinus*" *acutidactylus*, *Eopinnacrinus*, and *Metabolocrinus*. These are all placed within the superfamily Merocrinacea and the families Merocrinidae and Metabolocrinidae, whereas previously they were all in separate families. The Merocrinidae have three or more (rarely one) primibrachials and isotomous arm branching, whereas the Metabolocrinidae (*Metabolocrinus* and *Eopinnacrinus*) have one primibrachial and pinnulate arm branching (see Systematic Paleontology, p. 21).

Finally, the cyathocrines are recognized as an order. Llanvirn to Caradoc cyathocrines are divisible into three groups: 1. *Eoparisocrinus* and *Illemocrinus* are primitive; 2. the specialized *Palaeocrinus-Porocrinus-Carabocrinus*-type crinoids; and 3. the specialized *Agostocrinus*. Moore, Lane, and Strimple (1978) and subsequent workers have placed nearly all of the cyathocrinid genera into separate families. In contrast, the analysis herein suggests that these are closely related crinoids. For the present, all Llanvirn cyathocrines are placed into one superfamily, the Cyathocrinitacea, and three families. *Eoparisocrinus* and *Illemocrinus* are in the Euspirocrinidae. Assignment of *Eoparisocrinus* follows Ausich (1986c) and Brower (1995a), but *Illemocrinus* is reassigned from the Thalamocrinidae (Eckert, 1987) to the Euspirocrinidae. All of the specialized pore-bearing forms are placed into a single family, Porocrinidae. The Porocrinidae is reassigned to the superfamily Cyathocrinitacea. This means that the Carabocrinidae is a junior synonym of the Porocrinidae. The similarities among these crinoids and members of the Sphaerocrinidae are regarded as convergence. The new family Agostocrinidae is erected for the unusual genus *Agostocrinus*.

These revisions place all elements of this initial cyathocrinid radiation into a single superfamily. Further phylogenetic study is required to determine the relationships of these taxa to younger cyathocrines that did not radiate until the Silurian and Devonian.

Camerates.—Arenig to Caradoc camerates are clearly divisible into diplobathrids and monobathrids as traditionally understood, and these are regarded as ordinal in rank (Moore and Laudon, 1943; Ubaghs, 1978c). Ubaghs (1953, 1978c) subdivided the Diplobathrida into the two suborders based on the position of the radial and basal circlets. If the basals were in the same circlet as the radials, he regarded them as zygodiplobathrids; whereas if basals were in a typical position beneath the radials, he regarded them as eudiplobathrids. Only two genera were assigned to the zygodiplobathrids by Ubaghs (1978c), *Cleiocrinus* (middle Ordovician) and *Spyridiocrinus* (Lower Devonian). Several authors (Brower, 1975; Kelly, Frest, and Strimple, 1978; Haugh, 1979; Kolata, 1982; Ausich, 1986a) questioned this distinction; and, despite the fact that *Cleiocrinus* is unusual, phylogenetic results here fail to support these two suborders. Consequently, this subordinal distinction is abandoned. Furthermore, although beyond the scope of this study, the superfamily rank of the Nyctocrinacea is ques-

Table 2. Crinoid classification by Simms and Sevastopulo (1993).

Class Crinoidea
Subclass Camerata
Order Diplobathrida
Order Monobathrida
Subclass Disparida
Subclass Cladida
"stem-group cladids"
Infraclass Cyathocrinina
Infraclass Flexibilia
Infraclass Articulata
Incertae Sedis ('Subclass') Hybocrinida

tioned. Without suborders and with consideration of the nyctocrinids as only a family, the diplobathrids are divisible into only two superfamilies, Rhodocrinitacea and Dimerocrinitacea (see Systematic Paleontology, p. 23–24).

Arenig to Caradoc rhodocrinitaceans are divided into four families. The most diverse family and the one requiring revision of Ubaghs's work (1978c) is the Rhodocrinitidae. Ubaghs (1978c) distinguished the Archaeocrinidae and Rhodocrinitidae, but Kolata (1982) combined these two families due to the lack of any clear identifying distinctions; Kolata's decision was followed by Ausich (1986a). I also suggest herein that the Arenig to Caradoc genera of these families are part of a single radiation and that it is not divided into rhodocrinitids and archaeocrinids (*sensu* Ubaghs, 1978c). Ubaghs (1978c) placed *Diabolocrinus, Paradiabolocrinus,* and *Trichinocrinus,* as well as many younger genera, into the Rhodocrinitidae, whereas the Archaeocrinidae included *Archaeocrinus, Balacrinus, Neoarchaeocrinus, Pararchaeocrinus,* and *Rhaphanocrinus.* (Note that *Proexenocrinus* was considered a monobathrid, and *Bromidocrinus, Cotylacrinna,* and *Simplococrinus* were described later.) Thus, the division of these genera by Ubaghs (1978c) does not correspond to the phylogenetic results presented herein. For the present, this family is called the Rhodocrinitidae.

Other Llanvirn to Caradoc families in the Rhodocrinitacea include the Anthracocrinidae with four genera (Fig. 9; see Systematic Paleontology, p. 24) and the monogeneric families Cleiocrinidae and Reteocrinidae. The Dimerocrinitidae, as defined by Ubaghs (1978c), is the only Arenig to Caradoc family in the Dimerocrinitacea, but this group diversified later.

With the exception of *Eopatelliocrinus,* all Arenig to Caradoc monobathrids are placed in the Glyptocrinidae. These are the oldest and most primitive members of the suborder Glyptocrinina (see Systematic Paleontology, p. 24). *Eopatelliocrinus* is the oldest member of the family Patelliocrinidae. The suborder Compsocrinina did not evolve until after the Caradoc.

Disparids.—Following Kelly (1982, 1986) and Simms and Sevastopulo (1993), the disparids are herein considered to be a subclass. They evolved through loss of the basal circlet from a four-circlet ancestor (Ausich, 1998a). Moore *et al.* (1978) subdivided disparids into superfamilies based largely on the position of the plane of bilateral symmetry through the crown, aboral cup shape, and radial facets. As a subclass, Disparida requires subdivision into orders. Based on the results herein, Early and middle Ordovician orders are defined on the basis of the presence or absence of plate circlets, number and position of radial plates, aboral cup symmetry and architecture, radial facets, and free arms. Accordingly, seven orders are recognized for the Ordovician disparids treated here (see Systematic Paleontology, p. 25–28). Five of these became established during the Arenig; the Hybocrinida evolved during the Llanvirn; and the Calceocrinida first appeared during the Caradoc. Undoubtedly, additional orders exist among younger disparids, but delineation of other orders is beyond the scope of the present study.

The Eustenocrinida contains crinoids with radials and infrabasals in every ray. Primitively, eustenocrinids have five radial plates and five infrabasal plates, but *Virucrinus* has only four plates in each circlet. This order contains two families (see Systematic Paleontology, p. 25 for diagnoses and discussions of each suprageneric category). The Eustenocrinidae has a single arm on each radial facet, whereas the Acolocrinidae has multiple armlets articulating on the radial facet. The order Maennilicrinida comprises four genera in one family; and, in addition to the basal circlet, they lost the entire radial circlet. These four genera are all from eastern Europe and, for the present, include two poorly known genera, *Pandoracrinus*

Table 3. Ordinal classification of the Crinoidea followed herein.

Class Crinoidea
Subclass Aethocrinea
Order Aethocrinida
Subclass Cladida
Order Dendrocrinida
Order Cyathocrinida
Order Poteriocrinida[1]
Subclass Flexibilia
Order Taxocrinida
Order Sagenocrinida
Subclass Articulata
Order Millericrinida
Order Cyrtocrinida
Order Bourgueticrinida
Order Isocrinida
Order Comatulida
Order Uintacrinida
Order Roveacrinid
Subclass Camerata
Order Diplobathrida
Order Monobathrida
Subclass Disparida[2]
Order Eustenocrinida
Order Maennilicrinida
Order Tetragonocrinida
Order Homocrinida
Order Calceocrinida
Order Myelodactyla
Order Hybocrinida

[1]The order Poteriocrinida may not be monophyletic and requires further study.
[2]The Disparida contains additional, younger orders not listed.

and *Vosekocrinus* (see Systematic Paleontology, p. 25–26). This order became extinct by the end of the Llanvirn (Fig. 1, 10), and these crinoids are not related to middle Paleozoic disparids that also lost all radials. The third small order is the Tetragonocrinida, which contains two genera, *Ramseyocrinus* and *Tetragonocrinus*, placed in a single family. These are exceedingly simplified, perhaps paedomorphic forms, that have only one circlet, the lintel circlet, in the aboral cup. Again, this order did not survive beyond the Llanvirn.

Ibexocrinus is the oldest known disparid to lose part of the radial circlet and represents the beginning of the major Early to middle Ordovician radiation of disparids, the order Homocrinida. It probably gave rise to "*Pariocrinus*," the oldest member of the Myelodactylida (Fig. 1, 10–11). It is possible that *Ibexocrinus* gave rise to the order Calceocrinida, but in Figures 10 and 11, the calceocrinids are depicted as having evolved from *Ectenocrinus* because this is most consistent with the stratigraphic occurrence of these genera. The order Homocrinida contains four families. The Homocrinidae is, as in the Homocrinacea (Moore and Lane, 1978b), composed of disparids with radial plates in the B, C, and E rays only (although one genus, *Difficilicrinus*, lost the C radial). In addition, radial facets are plenary, typically four to five primibrachials occur, and more than ten nonpinnulate arms are present. From this design, members of this order iteratively lost the B radial three times (Fig. 7.1, 10–11), and each of these separate evolutionary events is regarded as a distinct family. During the Arenig the monogeneric family Othneiocrinidae arose through loss of the B radial, change in radial facets, variable primibrachial number, and development of ten pinnulate arms. During the Llanvirn, the Cincinnaticrinidae arose with *Isotomocrinus* as the oldest known representative. These are essentially the Heterocrinacea of Moore and Lane (1978a) and the Cincinnaticrinacea of Warn and Strimple (1977), and this family is characterized by the loss of the B radial, restriction to four or five primibrachials (with one possible exception), and retention of more than ten nonpinnulate arms.

The fourth family of the order Homocrinida is the Columbicrinidae, which arose during the Caradoc by loss of the B radial, retention of plenary radial facets, limitation of one to three primibrachials, and development of ten pinnulate arms.

The order Calceocrinida is morphologically unique with no clear transitional or ancestral forms, so it is difficult to determine its origin. *Cremacrinus* with four arms and three (rather than one or two) radials is regarded as the most primitive calceocrinid, and because it contains B, C, and E radials, it has been thought to have had a homocrinid origin (Moore, 1962). Due to the deep rooting of this group in the cladogram of Figure 6 and the highly specialized morphology, these crinoids are considered to be an order. Similar to *Othneiocrinus*, the calceocrinids evolved a cup with different types of facets and unusual arms, although in calceocrinids the rays affected were different, the arm branching was a bilateral heterotomy, and a movable hinge developed between the lintels and the infrabasal-radial circlet.

During the Early and middle Ordovician, the order Myelodactylida had one family (Iocrinidae) represented by five genera. It is characterized principally by an erect crown, only the C radial in the radial circlet, and numerous arm branches. The order Hybocrinida probably arose from "*Pariocrinus*" and comprises six genera divided into three families (see Systematic Paleontology, p. 27–28).

DISCUSSION

The underlying assumption herein is that the phylogeny and classification of Early and middle Ordovician crinoids should be defined by the characters and character combinations of these crinoids largely independently of younger crinoids. This approach is different from the rationale of previous studies of crinoid phylogeny and classification and yields somewhat different results. This study reveals that a substantial degree of iterative evolution occurred among crinoids during this earliest history. For example, pinnulate arms evolved in many groups; ray plates were fixed into the calyx in camerates, flexibles, and some cladids; and pore structures appeared in several groups.

In the *Treatise* classification (Moore and Teichert, 1978), many of these early crinoid genera were either placed in monogeneric families or as the oldest member of an otherwise middle Paleozoic family. Certainly, a few highly unusual monogeneric families are still recognized; but the primary perspective for interpreting this phylogeny and classification is that these Ordovician radiations may not have any relationship to younger crinoids. This must be determined by phylogenetic study of crinoid lineages through the end-Ordovician extinctions. Some of these Early and middle Ordovician genera represent the origination of a clade that diversified later, such as *Euptychocrinus* for the Dimerocrinitidae and *Protaxocrinus* for the Flexibilia. Many genera, however, especially among the cladids, are reassigned to Ordovician families.

Although I follow the revised homologies of Ausich (1996a) herein, the phylogenetic analyses within the subclasses that are presented here should be independent of conflicts about ideas concerning homologies (Ausich, 1996a; Moore and Teichert, 1978). A study of this nature may require reexamination if new Early and middle Ordovician faunas are described with markedly different morphologies.

SYSTEMATIC PALEONTOLOGY

Class CRINOIDEA J. S. Miller, 1821

Discussion.—The crinoid classification proposed here uses the subclass classification of Ausich (1998a). A summary of the systematic changes suggested here for Early and middle Ordovician crinoids is as follows. As described by Ausich (1998a), six subclasses are recognized within the

Crinoidea; and *Aethocrinus*, formerly a cladid, and *Perittocrinus* and *Tetracionocrinus*, formerly disparids, are placed in the subclass Aethocrinea.

Within the Cladida a new family of the Cyathocrinitacea is formally recognized, the Agostocrinidae, which was previously considered a disparid group. *Archaetaxocrinus* is reassigned from the flexibles to the cladids, and *Colpodecrinus* and Colpodecrinidae Sprinkle and Kolata are reassigned from the camerates to the cladids. Cupulocrinidae Moore and Laudon is reassigned to the Dendrocrinacea, and Porocrinidae Miller and Gurley is reassigned to the Cyathocrinitacea. Familial reassignments of genera include *Agostocrinus* to the Agostocrinidae, *Archaetaxocrinus* to the Colpodecrinidae, *Quinquecaudex* to the Cupulocrinidae, *Ottawacrinus* to the Dendrocrinidae, *Illemocrinus* to the Euspirocrinidae, *Polycrinus* and *Praecupulocrinus* to the Merocrinidae, *Eopinnacrinus* to the Metabolocrinidae, and *Palaeocrinus* and *Carabocrinus* to the Porocrinidae. Assignment of junior synonyms include the following: Ottawacrinidae Moore and Laudon is a junior synonym of Dendrocrinidae, and Carabocrinidae Bather is a junior synonym of Porocrinidae. Finally, Ontariocrinidae Jaekel is considered a *nomen dubium*.

Within the Camerata the subordinal distinction of Ubaghs (1978c; zygodiplobathrids and eudiplobathrids) is not followed. The Cleiocrinidae is reassigned to the Rhodocrinitacea. Familial reassignments of genera to the Rhodocrinitidae include *Archaeocrinus, Balacrinus, Neoarchaeocrinus, Pararchaeocrinus, Rhaphanocrinus, Simplococrinus,* and *Spyridiocrinus. Celtocrinus* is assigned to the Glyptocrinidae. Assignment of junior synonyms includes the following: Archaeocrinidae Moore and Laudon and Spyridiocrinidae Jaekel are junior synonyms of the Rhodocrinitidae, and Nyctocrinacea Moore and Laudon is a junior synonym of the Dimerocrinitacea.

Within the Disparida is the new order Maennilicrinida; the new orders Eustenocrinida and Tetragonocrinida, having previously been regarded as subfamilies; and the new orders Homocrinida, Calceocrinida, and Myelodactylida, having previously been regarded as superfamilies. New taxa recognized herein are the following: Maennilicrinidae and Columbicrinidae as well as the *nomen translatum* Atopocrinidae Warn and Strimple. *Pandoracrinus* is reassigned from the cladids to the disparids. *Baerocrinus* is considered to be teratological; thus the Baerocrinidae is regarded as a *nomen dubium*. The Acolocrinidae is now in the Eustenocrinida; the Tetragonocrinidae is reassigned from the Myelodactylacea to the Tetragonocrinida; and the superfamilies Homocrinitacea and Cincinnaticrinitacea are no longer recognized. Familial reassignments of genera include *Othneiocrinus* to the Atopocrinidae; *Glaucocrinus* questionably to the Cincinnaticrinidae; *Columbicrinus, Geraocrinus,* and *Praecursoricrinus* to the Columbicrinidae; *Apodasmocrinus, Difficilicrinus,* and *Tunguskocrinus* to the Homocrinidae; *Tornatilicrinus* to the Iocrinidae; *Maennilicrinus, Pandoracrinus, Pultivocrinus,* and *Vosekocrinus* to the Maennilicrinidae; *Ramseyocrinus* to the Tetragonocrinidae. Assignment of junior synonyms include the following: Apodasmocrinidae, Daedalocrininae, Homocrininae, and Tunguskocrinidae are junior synonyms of Homocrinidae; Ramseycrinidae is the junior synonym of Tetragonocrinidae; Tryssocrininae and Atopocrininae are junior synonyms of the Cincinnaticrinidae; and Tornatilicrinidae is a junior synonym of Iocrinidae.

Subclass AETHOCRINEA Ausich, 1998

Diagnosis.—Aboral cup composed of lintels, infrabasals, basals, and radials; aboral cup plates sutured closely; proximal brachials free or fixed; proximal interradials may be incorporated in aboral cup; tegmen not rigid; mouth probably subtegminal; anus through tegmen; posterior portion with extra plating; pore structures may be present; free arms uniserial, nonpinnulate, imperforate.

Discussion.—See Ausich, 1998a.

Order AETHOCRINIDA Ausich, 1998

Diagnosis.—Same as subclass.

Included families.—Family Aethocrinidae Ubaghs and Perittocrinidae Abel.

Family AETHOCRINIDAE Ubaghs, 1969

Diagnosis.—Aethocrinid with lintels, infrabasals, basals, and radials all large cup plates; five lintels and infrabasals; first primibrachial partially incorporated into calyx; superradianal and inferradianal nearly same size; pore structures absent; column pentameric.

Discussion.—See Ausich, 1998a.

Included genus.—*Aethocrinus* Ubaghs.

Family PERITTOCRINIDAE Abel, 1920

Diagnosis.—Aethocrinid with lintels and radials as large cup plates, infrabasals and basals small cup plates; four lintels and infrabasals; first primibrachials free; inferradianal much larger than superradianal; pore structures may be present, column tetrameric.

Discussion.—See Ausich, 1998a.

Included genera.—*Perittocrinus* Jaekel and *Tetracionocrinus* Ubaghs.

Subclass CLADIDA Moore and Laudon, 1943

Diagnosis.—Aboral cup primitively composed of infrabasals, basals, and radials; aboral cup plates sutured closely; proximal brachials primitively free, fixed in a few derived forms; proximal interradials primitively not incorporated in aboral cup, incorporated in some derived forms; tegmen not rigid; mouth subtegminal; anus through tegmen, from anal sac, or through aboral cup; primitively posterior portion with extra plating, no extra plating in some derived forms; pore structures may be present; free arms uniserial, nonpinnulate or pinnulate, imperforate.

Discussion.—The elevation of the Cladida to subclass status by Kelly (1982, 1986) and Simms and Sevastopulo

(1993) is followed here. Two orders appeared early in the Ordovician, the Dendrocrinida and the Cyathocrinida. The pinnulate cladids were placed in an equally ranked category by Moore, Lane, and Strimple (1978) as the poteriocrinids. The monophyletic nature of this grouping has been widely questioned (McIntosh, 1986; Sevastopulo and Lane, 1988; Simms and Sevastopulo, 1993; and others). Resolution of the disposition of these advanced cladids awaits phylogenetic analyses of Devonian forms and cannot be addressed here.

Order DENDROCRINIDA Bather, 1899

[*nom. transl.* Ausich, herein, *ex* Dendrocrinina Bather, 1899]

Diagnosis.—Aboral cup low to medium cone or low to high bowl shaped, plate sculpturing variable; radial facets angustary to plenary; anal sac tall, cylindrical or inflated, may be porous, may have conspicuous plicate plates; arms rectangular or cuneate uniserial brachials in early forms, nonpinnulate or pinnulate, isotomous or heterotomous arm branching; tegmen plates poorly sutured, presumably composed of small plates, orals not prominent; pore structures typically absent, rarely present in early forms.

Discussion.—The Dendrocrinida is considered to be the primitive, basic stock of cladids from which other monophyletic groups were derived (Lane, 1978b). Thus, the Dendrocrinida is a paraphyletic group with camerates, flexibles, and cyathocrines derived from them. In addition, the advanced cladids, the pinnulate poteriocrines of Moore and Teichert (1978), were derived from the dendrocrines. The phylogenetic and taxonomic status of the former is uncertain and beyond the scope of my study, as discussed above.

Superfamily DENDROCRINACEA Bather, 1899

Diagnosis.—Aboral cup high to medium; infrabasals high; radial facets angustary to plenary; radianal compound or simple, if simple, not full proximal width of C radial; fixed brachials and interradials present or absent; three or more primibrachials; arm branching isotomous or heterotomous.

Discussion.—Early and middle Ordovician Dendrocrininea include the Dendrocrinidae, Colpodecrinidae (previously assigned to the Camerata), and the Cupulocrinidae (previously assigned to the Merocrinacea). In addition, the Ottawacrinidae, previously regarded as a merocrinacean, is considered to be a junior synonym of the Dendrocrinidae.

Family DENDROCRINIDAE Wachsmuth and Springer, 1886

Ottawacrinidae Moore and Laudon, 1943.

Diagnosis.—Radial facets angustary, radianal compound or simple; pore structures, fixed brachials, interradials absent; three to eight primibrachials.

Discussion.—The concept of this family is essentially unchanged from that of Moore and Lane (1978c) and subsequent authors. A new cladid genus to be described by Ausich, Bolton, and Cumming (1998) is also considered herein. The genus *Ottawacrinus,* however, is reassigned to the Dendrocrinidae, which makes the Ottawacrinidae a junior synonym of the Dendrocrinidae. Also, one Early to middle Ordovician genus, *Quinquecaudex,* is removed from this family and placed within the Cupulocrinidae.

Included genera.—*Dendrocrinus* Hall, *Brechmocrinus* Ausich, Bolton, and Cumming, *Compagicrinus* Jobson and Paul, *Elpasocrinus* Sprinkle and Wahlman, *Esthonocrinus* Jaekel, *Grenprisia* Moore, *Ottawacrinus* Billings, and *Plicodendrocrinus* Brower are Early and middle Ordovician genera.

Family COLPODECRINIDAE Sprinkle and Kolata, 1982

Diagnosis.—Radial facets fixed peneplenary, radianal simple or compound, pore structures present or absent, fixed brachials and interradials present, three primibrachials.

Discussion.—This family is retained to include *Archaetaxocrinus* and *Colpodecrinus,* which are believed to represent a Llanvirn divergence from the basic dendrocrinid design. *Colpodecrinus* differs in many respects from *Archaetaxocrinus,* but it is more likely to have evolved from this genus than from any other. Of the rearrangement of genera into higher categories presented here for cladids, this is the most problematic.

Sprinkle and Kolata (1982) placed this very unusual crinoid into the Camerata; however, *Colpodecrinus* and Colpodecrinidae are reassigned herein to the Cladida. *Colpodecrinus* is considered herein to be a cladid rather than a camerate (Sprinkle and Kolata, 1982) because the posterior interray is unlike camerates, and most Caradoc camerates have biserial arms. The posterior interray of *Colpodecrinus* is reinterpreted as having four infrabasal plates, four basal plates, five radial plates with the C radial small, radianal, anal X, and fixed brachials and interradials. The radianal and anal X interrupt the radial circlet, and the hexagonal radianal supports the anal X above to the left and the small C radial above to the right. By placing *Archaetaxocrinus* in the Colpodecrinidae, it is reassigned from its previous position in the Taxocrinidae.

Included genera.—*Colpodecrinus* Sprinkle and Kolata and *Archaetaxocrinus* Lewis.

Family CUPULOCRINIDAE Moore and Laudon, 1943

Diagnosis.—Radial facets peneplenary to plenary; radianal simple; pore structures absent; fixed brachials absent, interradials present or absent; three or four primibrachials.

Discussion.—The family Cupulocrinidae is redefined to include *Cupulocrinus* and *Quinquecaudex,* which represent a radiation away from the dendrocrinid lineage toward the flexibles. Two morphological changes characterize this transition: incorporation of fixed interradial plates into the calyx, and widening of radial facets from angustary to plenary. Although *Quinquecaudex* has angustary radial facets like dendrocrinids, the incorporation of fixed interradials distinguishes it from these forms. *Cupulocrinus* has both of these advanced features. *Praecupulocrinus* is reassigned to the Merocrinidae.

Included genera.—Cupulocrinus d'Orbigny and *Quinquecaudex* Brower and Veinus.

Superfamily MEROCRINACEA S. A. Miller, 1890

Diagnosis.—Aboral cup low conical; infrabasals low; radial facets peneplenary to plenary; radianal simple, full proximal width of C radial; fixed brachials and interradials absent; one to many primibrachials; arm branching isotomous, heterotomous, or endotomous.

Discussion.—Early and middle Ordovician families of the Merocrinacea include the Merocrinidae and Metabolocrinidae. The Cupulocrinidae are reassigned to the Dendrocrinacea, the Ottawacrinidae is considered a junior synonym of the Dendrocrinidae, and the Ontariocrinidae is considered to be a *nomen dubium.*

Family MEROCRINIDAE S. A. Miller, 1890

Diagnosis.—Three or more (rarely one) primibrachials; isotomous arm branching.

Discussion.—Three additional taxa are assigned to this family, which was previously monogeneric. These are *Praecupulocrinus* from the Cupulocrinidae, *Polycrinus* from the Mastigocrinidae, and "*Dendrocrinus*" *acutidactylus.* "*Dendrocrinus*" *acutidactylus* does not belong to *Dendrocrinus* and probably represents a new genus. All of these taxa share the diagnostic characters of the Merocrinidae and, thus, they are considered to be the result of a single small radiation.

Included genera.—Merocrinus Walcott, *Praecupulocrinus* Brower, *Polycrinus* Jaekel, and "*Dendrocrinus*" *acutidactylus* Billings.

Family ONTARIOCRINIDAE Jaekel, 1918

Discussion.—Because the genus on which this family was founded has unknown taxonomic status, this family should be regarded as a *nomen dubium.*

Included genus.—Ontariocrinus Jaekel.

Family METABOLOCRINIDAE Jaekel, 1918

Diagnosis.—One primibrachial, arms endotomously pinnulate.

Discussion.—This family has members with the unique combination of one primibrachial and endotomously pinnulate arm branching. *Eopinnacrinus* is reassigned to this family from the Botryocrinidae. Despite the fact that these genera are from distinct geographic areas, the unique morphology is considered to record evolutionary descent.

Included genera.—Metabolocrinus Jaekel and *Eopinnacrinus* Brower and Veinus.

Superfamily MASTIGOCRINACEA Jaekel, 1918

Discussion.—Details of this superfamily are not treated here, but *Polycrinus* is reassigned from the Mastigocrinidae to the Merocrinidae.

Order CYATHOCRINIDA Bather, 1899

[*nom. transl.* Ausich, herein, *ex* Cyathocrinina Bather, 1899]

Diagnosis.—Aboral cup medium cone, bowl, or globe shaped; primitively plate sculpturing stellate; radial facets angustary; anal sac absent or short, nonporous; if absent, anal sac flush with tegmen or on side of aboral cup, arms rectangular uniserial; brachials nonpinnulate; atomous, isotomous, or heterotomous arm branching; tegmen plates well sutured, typically composed of large plates, orals prominent; pore structures present or absent in early forms, absent in later forms.

Discussion.—The Cyathocrinida is a monophyletic clade that deviated from the Dendrocrinida both by assuming only a restricted subset of dendrocrinid morphological variations and by evolving new morphologies. Many of these early distinctions are blurred as cyathocrines diversified later during the Paleozoic. Examples of restricted morphological variance include angustary radial facets, stellate aboral plate sculpturing, rectangular uniserial brachials, and nonpinnulate arms. New features of early cyathocrines include globe-shaped aboral cups in some, reduction of the anal sac to either a small feature or complete elimination, a tegmen with well-sutured, prominent oral plates, and pore structures in many genera.

Lane and Moore (1978) subdivided the Cyathocrinina into three superfamilies, the Cyathocrinitacea, the Gasterocomina, and the Codiacrinacea. Middle Ordovician genera were placed in both the Cyathocrinitacea and the Gasterocomina, and the principal distinction between these two superfamilies was that the former had an anal sac and the latter had an anal opening flush on the tegmen or cup. Accordingly, *Porocrinus, Palaeocrinus, Carabocrinus, and Triboloporus,* which lack an anal sac, were placed in the Gasterocomina. There are no known crinoids that link these Ordovician crinoids to younger gasterocominids, and the one gasterocominid that is alleged to be similar, *Sphaerocrinus* (Lane & Moore, 1978), is actually quite different. My interpretation is that the anal sac was lost in two different lineages of Cyathocrinitacea, once in the Ordovician porocrinids, also characterized by pore structures, and a second time in Silurian and Devonian forms. A better, revised diagnosis of the Gasterocomina requires phylogenetic analysis of Silurian and Devonian cyathocrines.

Superfamily CYATHOCRINITACEA Bassler, 1938

Diagnosis.—Aboral cup cone, bowl, or globe shaped, five or three infrabasals, five radials; radianal simple, compound, or absent; anal X large; tegmen with slender anal sac or anal opening flush on tegmen; pore structures present or absent; arm branching isotomous, rarely heterotomous.

Family EUSPIROCRINIDAE Bather, 1890

Diagnosis.—Aboral cup cone or bowl shaped; three or five infrabasals; radial facets large; radianal simple; radial facets narrow to wide angustary; no pore structures; two or three anal plates in cup, radianal tetragonal or pentagonal; anal sac high; arms erect, isotomous arm branching.

Discussion.—Two Early and middle Ordovician genera are assigned to this family. Previously, *Illemocrinus* was assigned to the Thalamocrinidae.

Included genera.—*Eoparisocrinus* Ausich and *Illemocrinus* Eckert are Early and middle Ordovician members.

Family THALAMOCRINIDAE Miller and Gurley, 1895

Discussion.—*Illemocrinus* Eckert is reassigned to the Euspirocrinidae, which restricts this family to early Silurian and younger representatives.

Family AGOSTOCRINIDAE new family

Diagnosis.—Aboral cup medium, cone shaped; three infrabasals; radial plates much reduced; aboral cup basically composed of infrabasals, basals, and radianal; radianal simple, in contact with infrabasals; radial facet fixed; no pore structures; anal X and anal opening on tegmen; recumbent arms, unusual heterotomous branching.

Discussion.—Kesling and Paul (1971) and Moore and Strimple (1978) considered *Agostocrinus* to be a highly unusual disparid and assigned it to the Catillocrinidae. This crinoid, however, has recumbent arms, not multiple facets on radial plates, so it is not similar to other catillocrinids. Termier and Termier (1972) suggested that *Agostocrinus* and *Acolocrinus* should be assigned to a single family and suggested that that family be the Agostocrinidae. *Acolocrinus* is now assigned to a distinct family, the Acolocrinidae (Brett, 1980), and is treated here as a disparid; but *Agostocrinus* is considered as a very unusual cladid. *Agostocrinus* is unusual because of the very reduced radials, recumbent arms, arm branching, and anal X. Although cladids with simple radianals, as interpreted for *Agostocrinus*, do not have the radianal in contact with the infrabasals, cladids with compound radianals do. As a cladid, *Agostocrinus* is interpreted as an unusual, early cyathocrine that left no descendants. The Agostocrinidae was never formally described by Termier and Termier (1972), and it is erected here for this unusual cladid.

Included genera.—*Agostocrinus* Kesling and Paul.

Family POROCRINIDAE Miller and Gurley, 1894

Carabocrinidae Bather, 1899.

Diagnosis.—Aboral cup cone to globe shaped; five infrabasals; anal X, radial plates large; radianal simple or compound; radial facets angustary; pore structures; no anal sac, anal opening in tegmen; arms erect, isotomous or atomous arm branching.

Discussion.—All of the conical to globose Llanvirn to Caradoc cyathocrinids with pore structures, well-sutured oral plates, and the anus on the tegmen or the side of the cup are regarded as a single evolutionary cluster of species. Accordingly, they belong to the same family rather than being divided among three families. As in other taxa, the presence of a compound radianal in *Carabocrinus* was considered by Lane and Moore (1978) to be sufficient to define a separate family, but in the lineage herein, this feature is considered to be only a generic-level character. With this interpretation, Carabocrinidae is regarded as a junior synonym of Porocrinidae. Also, *Palaeocrinus* is reassigned from the Sphaerocrinidae to the Porocrinidae. Furthermore this family is reassigned to the Cyathocrinitacea from the Gasterocomacea.

Included genera.—*Porocrinus* Billings, *Carabocrinus* Billings, *Palaeocrinus* Billings, and *Triboloporus* Kesling and Paul.

Superfamily GASTEROCOMACEA Roemer, 1854

[*nom. transl.* Moore and Lane in Moore and Strimple, 1973, p. 18, *ex* Gasterocomidae Roemer, 1854, p. 299]

Diagnosis.—Aboral cup bowl to globe shaped; five, three, or one infrabasal; five radials; anal X present or absent; radianal simple if present; anus flush with tegmen and on tegmen or on side of aboral cup, no anal sac; pore structures absent; arm branching isotomous or atomous.

Discussion.—The Porocrinidae is reassigned from this superfamily to the Cyathocrinitacea. Thus, Gasterocomina is now confined to Devonian and younger forms.

Family GASTEROCOMIDAE Roemer, 1854

Discussion.—Details of this family are not treated here.

Family SPHAEROCRINIDAE Jaekel, 1895

Diagnosis.—Details of this family are not treated here.

Discussion.—With removal of *Palaeocrinus* from this family, it is restricted to the Devonian.

Family CROTALOCRINITIDAE Bassler, 1938

Discussion.—Details of this family are not treated here.

Superfamily CODIACRINACEA Bather, 1890

Discussion.—The details of this superfamily are not treated here.

Order POTERIOCRINIDA Jaekel, 1918

[*nom. transl.* Ausich, herein, *ex* Poteriocrinina Jaekel, 1918]

Discussion.—Details of these advanced cladids are not treated here because they are younger than the Caradoc. This grouping of crinoids, as organized by Moore, Lane, and Strimple (1978) is undoubtedly polyphyletic to some extent, as suggested by McIntosh (1986), Sevastopulo and Lane (1988), and Simms and Sevastopulo (1993), among others.

Subclass FLEXIBILIA von Zittel, 1895

Diagnosis.—Aboral cup composed of infrabasals (primitively three, fewer in some derived forms), basals, and radials; aboral cup plates sutured loosely; proximal brachials fixed primitively or free in some derived forms; proximal interradials incorporated primitively in aboral cup, not incorporated in some derived forms; tegmen flexible; mouth on tegmen; anus through tegmen; posterior portion with extra plating primitively, no extra plates in some derived forms; pore structures absent; free arms uniserial, nonpinnulate, imperforate.

Discussion.—*Archaetaxocrinus* is removed from the Flexibilia to the Cladida, an interpretation that follows traditional views on the origins of flexible crinoids from *Cupulocrinus* during the Caradoc (Springer, 1911). See discussion in the phylogeny section above, p. 5.

Order TAXOCRINIDA Springer, 1913

Discussion.—Only *Taxocrinus* and *Protaxocrinus* are treated here.

Superfamily TAXOCRINACEA Angelin, 1878

Family TAXOCRINIDAE Angelin, 1878

Diagnosis.—See Moore, 1978.

Included genera.—*Taxocrinus* Phillips and *Protaxocrinus* Springer. Further phylogenetic analyses are required to determine whether the remaining Taxocrinidae of Moore (1978) belong with these genera or elsewhere. *Archaetaxocrinus* is reassigned to the Colpodecrinidae.

Order SAGENOCRINIDA Springer, 1913

Discussion.—Details of this order are not treated here.

Subclass ARTICULATA von Zittel, 1879

Diagnosis.—Aboral cup composed primitively of infrabasals, basals, and radials, few in derived forms; aboral cup plates sutured closely; proximal brachials free primitively, fixed in some derived forms; proximal interradials not incorporated primitively in aboral cup, incorporated in some derived forms; tegmen not rigid; mouth on tegmen; anus through tegmen; posterior portion with no extra plating; pore structures absent; free arms uniserial, pinnulate, perforate.

Discussion.—Details of this subclass are not treated here.

Subclass CAMERATA Wachsmuth and Springer, 1885

Diagnosis.—Aboral cup composed of infrabasals, basals, and radials or of basals and radials; aboral cup plates sutured rigidly; proximal brachials fixed primitively, free in some derived forms; proximal interradials incorporated in aboral cup primitively, not incorporated in some derived forms; tegmen rigid; mouth subtegminal; anus through tegmen or anal tube; posterior portion with extra plating primitively, no extra plates in some derived forms; pore structures absent; free arms uniserial, nonpinnulate, imperforate primitively, in derived forms biserial and pinnulate.

Order DIPLOBATHRIDA Moore and Laudon, 1943

Diagnosis.—Camerates with aboral cup composed primitively of infrabasals, basals, and radial plates.

Discussion.—As discussed above, the suborder distinction (zygodiplobathrids and eudiplobathrids) of Ubaghs (1978c) is not followed. *Cleiocrinus* is placed in its own family in the Rhodocrinitacea, and *Spyridiocrinus* is probably also a Rhodocrinitidae.

Superfamily RHODOCRINITACEA Roemer, 1855

Diagnosis.—Diplobathrid with radials separated in all rays by sutural contact between the first plate in interray and the basal plate.

Discussion.—A distinction between the Rhodocrinitidae and the Archaeocrinidae is not made; see discussion below.

Included families.—Rhodocrinitidae Roemer, Anthracocrinidae Strimple and Watkins, Reteocrinidae Wachsmuth and Springer, and Cleiocrinidae S. A. Miller are Early and middle Ordovician families supported by phylogenetic interpretations herein. Verification of Opsiocrinidae Kier and Anthemocrinidae Jaekel that were recognized in this superfamily by Ubaghs (1978c) requires phylogenetic analysis of younger genera.

Family RHODOCRINITIDAE Roemer, 1855

Archaeocrinidae Moore and Laudon, 1943.
Spyridiocrinidae Jaekel, 1918.

Diagnosis.—Calyx globular, conical, or bowl shaped; basal concavity shallow or absent; interradial plates large, regular, in contact with tegmen; anitaxis primitively absent in some derived forms; no pores through calyx; some fixed arm plates; weblike extension of fixed brachials and pinnulars absent; arms uniserial or biserial, pinnulate.

Discussion.—Kolata (1982) combined the Rhodocrinitidae and Archaeocrinidae to form one family ranging from the Early Ordovician to the early Mississippian. Until further study of younger genera demonstrates otherwise, I follow Kolata's (1982) classification, and the Rhodocrinitidae has priority. It is quite possible, however, that these Ordovician genera, perhaps with some Silurian genera, represent a single clade that is distinct from later forms and that these should be separated at the family level from younger genera in the Rhodocrinitidae as constituted here. If so, Archaeocrinidae would be an appropriate family for the older forms. The following reassignments are made: *Archaeocrinus, Balacrinus, Neoarchaeocrinus, Pararchaeocrinus, Rhaphanocrinus,* and *Simplococrinus* are reassigned from the Archaeocrinidae to the Rhodocrinitidae; *Spyridiocrinus,* a Devonian zygodiplobathrid (Ubaghs, 1978c) is also reassigned to the Rhodocrinitidae. At present, two families are regarded as junior synonyms of Rhodocrinitidae. These are Archaeocrinidae, as discussed above, and Spyridiocrinidae, because *Spyridiocrinus* is assigned to the Rhodocrinitidae.

Included genera.—Arenig to Caradoc genera that belong in the Rhodocrinitidae are *Archaeocrinus* Wachsmuth and Springer, *Balacrinus* Ramsbottom, *Bromidocrinus* Kolata, *Cotylacrinna* Brower, *Crinerocrinus* Kolata, *Diabolocrinus* Wachsmuth and Springer, *Neoarchaeocrinus* Strimple and Watkins, *Pararchaeocrinus* Strimple and Watkins, *Paradiabolocrinus* Brower and Veinus, *Proexenocrinus* Strimple and McGinnis, *Rhaphanocrinus* Wachsmuth and Springer, *Simplococrinus* Frest, Strimple, and Kelly, and *Trichinocrinus* Moore and Laudon. Twenty-one additional genera are currently assigned to this family (Ubaghs, 1978c; Kolata, 1982; Ausich, 1986a), and *Spyridiocrinus* should also be assigned here.

Family ANTHRACOCRINIDAE Strimple and Watkins, 1955

Diagnosis.—Calyx conical to bowl shaped, deep basal concavity; interradial plates large, regular; not in contact with tegmen; anitaxis absent; no pores through calyx; some fixed arm plates; weblike extension at the base of arms formed by fixed brachials and pinnulars; arms uniserial or biserial, pinnulate.

Included genera.—*Anthracocrinus* Strimple and Watkins, *Deocrinus* Hudson, *Gustabilicrinus* Guensburg, and *Hercocrinus* Hudson.

Family RETEOCRINIDAE Wachsmuth and Springer, 1885

Diagnosis.—Calyx conical; basal concavity absent; interradial plates small, irregular, in contact with tegmen; anitaxis present; no pores through calyx; some fixed arm plates; weblike extension of fixed brachials and pinnulars absent; arms uniserial, pinnulate or nonpinnulate.

Included genera.—*Reteocrinus* Wachsmuth and Springer is the only genus demonstrated herein to belong to this family. Further phylogenetic analyses are required to determine whether *Gaurocrinus* S. A. Miller belongs in this family or elsewhere.

Family CLEIOCRINIDAE S. A. Miller, 1890

Diagnosis.—Calyx conical, deep basal concavity; interradial plates absent; anitaxis present; pores through calyx, extremely numerous fixed brachials in weblike extension; arms uniserial, pinnulate.

Discussion.—This family is moved to the Rhodocrinitacea from the Zygodiplobathrida, the latter being dissolved.

Included genera.—*Cleiocrinus* Billings.

Family OPSIOCRINIDAE Kier, 1952

Discussion.—Details of this family are not treated here.

Family ANTHEMOCRINIDAE Jaekel, 1918

Discussion.—Details of this family are not treated here.

Superfamily DIMEROCRINITACEA von Zittel, 1879

Nyctocrinacea Moore and Laudon, 1943.

Diagnosis.—Diplobathrid with radials primitively separated only in the CD interray where primanal and the CD basal plate in sutural contact, in derived forms radials in contact in all interrays.

Discussion.—The definition of this superfamily follows Ubaghs (1978c) with the exception that the Nyctocrinidae is included within rather than being a separate superfamily. Thus Nyctocrinacea Moore and Laudon is considered to be a junior synonym of Dimerocrinitacea.

Included families.—Dimerocrinitidae Zittel, Lampterocrinidae Bather, Gazacrinidae S. A. Miller, Orthocrinidae Jaekel, and Nyctocrinidae Moore and Laudon.

Family DIMEROCRINITIDAE von Zittel, 1879

Diagnosis.—See Ubaghs, 1978c.

Included genera.—*Dimerocrinites* Phillips and *Euptychocrinus* Brower. Further phylogenetic analyses are required to determine whether the remaining Dimerocrinitidae of Ubaghs (1978c) belong with these genera or elsewhere.

Family LAMPTEROCRINIDAE Bather, 1899

Discussion.—Details of this family are not treated here.

Family GAZACRINIDAE S. A. Miller, 1892

Discussion.—Details of this family are not treated here.

Family ORTHOCRINIDAE Jaekel, 1918

Discussion.—Details of this family are not treated here.

Family NYCTOCRINIDAE Moore and Laudon, 1943

Discussion.—Details of this family are not treated here.

Order MONOBATHRIDA Moore and Laudon, 1943

Diagnosis.—Camerates with aboral cup composed of basals and radial plates.

Suborder COMPSOCRININA Ubaghs, 1978c

Diagnosis.—Monobathrid with hexagonal basal circlet; radials separated only in CD interray where primanal and the CD basal plate are in sutural contact.

Discussion.—Details of this suborder are not treated here.

Suborder GLYPTOCRININA Moore, 1952

Diagnosis.—Monobathrid with pentagonal basal circlet; radials adjoining in all interrays because primanal in sutural contact with C and D basal plates.

Superfamily GLYPTOCRINACEA von Zittel, 1879

Diagnosis.—See Ubaghs, 1978c.

Included family.—Glyptocrinidae von Zittel.

Family GLYPTOCRINIDAE von Zittel, 1879

Diagnosis.—See Ubaghs, 1978c.

Discussion.—*Celtocrinus,* previously left unassigned within the monobathrids (Donovan and Cope, 1989), is assigned to the Glyptocrinidae.

Included genera.—*Glyptocrinus* Hall, *Abludoglyptocrinus* Kolata, *Celtocrinus* Donovan and Cope, *Periglyptocrinus* Wachsmuth and Springer, *Pycnocrinus* S. A. Miller, and *Schizocrinus* Hall.

Superfamily PATELLIOCRINACEA Angelin, 1878

Diagnosis.—See Ubaghs, 1978c.

Family PATELLIOCRINIDAE Angelin, 1878

Diagnosis.—See Ubaghs, 1978c.

Included genera.—*Patelliocrinus* Angelin and *Eopatelliocrinus* Brower. Further phylogenetic analyses are required to determine whether the remaining Patelliocrinidae of Ubaghs (1978c) belong with these genera or elsewhere.

Family STELIDIOCRINIDAE Angelin, 1878

Discussion.—Details of this family are not treated here.

Superfamily MELOCRINITACEA d'Orbigny, 1852

Discussion.—Details of this superfamily are not treated here.

Superfamily PLATYCRINITACEA Austin and Austin, 1842

Discussion.—Details of this superfamily are not treated here.

Subclass DISPARIDA Moore and Laudon, 1943

Diagnosis.—Aboral cup composed of lintels, infrabasals, and a varying number of radials, primitively five but varies from five to none; aboral cup plates typically sutured rigidly; proximal brachials free; proximal interradials not incorporated in aboral cup; tegmen not rigid; mouth subtegminal; anus through tegmen or on anal sac; posterior portion with extra plating primitively, no extra plating in some derived forms; pore structures may be present; free arms uniserial, nonpinnulate, imperforate primitively, pinnulate in some derived forms.

Discussion.—The interpretation of homology of aboral cup plates used here follows Ausich (1996a); therefore the lowest two circlets of the disparid aboral cup are the lintels and infrabasals. If superradials (*sensu* Ubaghs, 1978a) are present, these are considered to be homologous to the radial circlet of other crinoids. With elevation of the Disparida to a subclass, superfamilies of Moore *et al.* (1978) are regarded as orders: Homocrinida, Calceocrinida, and Myelodactylida. In addition, other new orders include the Eustenocrinida, Tetragonocrinida, and Maennilicrinida; and the order Hybocrinida is maintained. The following higher-level groups are not retained: Tunguskocrinidae and Cincinnaticrinacea.

Order EUSTENOCRINIDA new order

Diagnosis.—Disparids with aboral cup composed of five lintels, five infrabasals, and five radials primitively, derived form with four infrabasals and radials; plate circlets symmetrical about oral-aboral axis; aboral cup medium cone shaped, radial facets peneplenary or plenary, and free arms branch.

Discussion.—The Eustenocrinidae was placed in the Myelodactylacea by Moore *et al.* (1978) along with the Iocrinidae and Myelodactylidae because all shared a crown bilateral symmetry on the A-CD crinoidal plane. In the present view of disparid evolution, however, the presence of radials rather than the plane of bilateral symmetry is key. The eustenocrinids are considered as primitive and represent a separate order with two families.

Included families.—Eustenocrinidae Ulrich and Acolocrinidae Brett.

Family EUSTENOCRINIDAE Ulrich, 1925

Diagnosis.—Five lintel plates; one arm per radial, arms may branch; radial processes and pore structures absent.

Discussion.—This family remains basically the same as defined by Moore *et al.* (1978) and as used by subsequent authors. *Pultivocrinus* is reassigned to the new order Maennilicrinida.

Included genera.—*Eustenocrinus* Ulrich, *Inyocrinus* Ausich, *Peniculocrinus* Moore, *Pogonipocrinus* Kelly and Ausich, *Ristnacrinus* Öpik, and *Virucrinus* Rozhnov.

Family ACOLOCRINIDAE Brett, 1980

Diagnosis.—Three lintel plates; multiple armlets per radial, arms atomous; radial processes present; pore structures present.

Discussion.—Brett (1980) recognized *Acolocrinus* as a distinctive crinoid and described the family Acolocrinidae to comprise *Acolocrinus* and *Paracolocrinus*. He considered *Acolocrinus* to be distinct from *Agostocrinus*, to which it had commonly been linked. Brett (1980) also considered *Acolocrinus* to be most probably an allagecrinacean but did not assign his new family to a superfamily. The fact that the acolocrinids have five radials and five infrabasals clearly aligns them with the order Eustenocrinida.

Included genera.—*Acolocrinus* Kesling and Paul and *Paracolocrinus* Brett.

Order MAENNILICRINIDA new order

Diagnosis.—Disparids with aboral cup composed of five lintels and five infrabasals; plate circlets symmetrical about oral-aboral axis; aboral cup cone or bowl shaped, radial facets peneplenary or plenary, and free arms branch.

Discussion.—This new order is designated for disparids that lost the entire radial circlet during the Arenig radiation. This order contains one family with four genera.

Included family.—Maennilicrinidae new family.

Family MAENNILICRINIDAE new family

Diagnosis.—Same as for order.

Discussion.—This new family unites genera that were previously assigned to several families. *Maennilicrinus* and *Vosekocrinus* were previously in the Iocrinidae, and *Pultivocrinus* was previously in the Eustenocrinidae. *Pandoracrinus* was questionably considered a cladid by Moore and Lane (1978c, p. 615), but it was linked with the disparid *Vosekocrinus*. Both of these crinoids are poorly known, but they appear to be similar and are placed within the Maennilicrinidae.

Included genera.—*Maennilicrinus* Rozhnov, *Pandoracrinus* Jaekel, *Pultivocrinus* Rozhnov, and *Vosekocrinus* Jaekel.

Order TETRAGONOCRINIDA new order

Diagnosis.—Disparids with aboral cup composed of a single circlet of four or five lintels; plate circlets symmetrical about oral-aboral axis; aboral cup low cone shaped, radial facets peneplenary or plenary, and free arms branch.

Discussion.—This order includes two very paedomorphic crinoids interpreted here to retain only one circlet, the lintel circlet, in the aboral cup.

Included family.—Tetragonocrinidae Stukalina.

Family TETRAGONOCRINIDAE Stukalina, 1980

Ramseyocrinidae Donovan, 1984.

Diagnosis.—Same as for order.

Discussion.—With *Tetragonocrinus* and *Ramseyocrinus* combined into a single family, Tetragonocrinidae Stukalina, 1980 is the senior synonym of Ramseyocrinidae Donovan, 1984. Previously, the Tetragonocrinidae was assigned to the superfamily Myelodactylacea, and the Ramseyocrinidae was unassigned to a superfamily.

Included genera.—*Ramseyocrinus* Bates and *Tetragonocrinus* Yeltyschwa.

Order HOMOCRINIDA new order

Diagnosis.—Disparids with aboral cup composed primitively of five lintels, five infrabasals, and three radials (B, C, and E rays), derived forms may lose radials; plate circlets symmetrical about oral-aboral axis; aboral cup cone or bowl shaped, radial facets primitively plenary, and free arms branch.

Discussion.—The Homocrinida is erected for a large number of Early and middle Ordovician crinoids that lost either two or three radial plates. This new order contains four families. Previously, the Homocrinidae was of superfamily rank. The Cincinnaticrinacea is no longer regarded to have rank above the family level and is in the Homocrinida. The Columbicrinidae is new and the Atopocrinidae is a *nomen translatum* from the subfamilial level.

Included families.—Homocrinidae Kirk, Cincinnaticrinidae Warn and Strimple, Columbicrinidae new family, and Atopocrinidae Warn and Strimple.

Family HOMOCRINIDAE Kirk, 1914

Apodasmocrinidae Frest, Strimple, and McGinnis, 1979.
Daedalocrininae Warn and Strimple, 1977.
Homocrininae Kirk, 1914.
Tunguskocrinidae Arendt, 1963.

Diagnosis.—B, C, and E radials primitive, C may be lost; radial facets plenary, all similar on an individual; two to nine primibrachials; more than ten nonpinnulate arms.

Discussion.—Genera assigned to the Homocrinidae were previously assigned to a variety of families and superfamilies. Reassignments include the following: *Apodasmocrinus* and *Difficilicrinus* were in the Apodasmocrinidae, *Daedalocrinus* was in the homocrinid subfamily Daedalocrininae, and *Tunguskocrinus* was in the Tunguskocrinidae within the Pisocrinacea. Previously, the Homocrinidae were divided into subfamilies (Warn and Strimple, 1977), but that distinction is not followed herein. Families and subfamilies now considered to be junior synonyms of the Homocrinidae are the Apodasmocrinidae, Daedalocrininae, Homocrininae, and Tunguskocrinidae.

Included genera.—*Apodasmocrinus* Frest, Strimple, and McGinnis, *Cataraquicrinus* Kolata, *Daedalocrinus* Ulrich, *Difficilicrinus* Frest, Strimple, and McGinnis, *Ectenocrinus* S. A. Miller, *Ibexocrinus* Lane, *Penicillicrinus* Warn, and *Tunguskocrinus* Arendt are Early and middle Ordovician genera considered herein as part of the Homocrinidae. Further phylogenetic analyses are required to determine whether the remaining Homocrinidae of Moore and Lane (1978b) belong with these genera or elsewhere, including *Homocrinus* Hall.

Family CINCINNATICRINIDAE Warn and Strimple, 1977

Atopocrininae Warn and Strimple, 1977.
Tryssocrininae Guensburg, 1984.

Diagnosis.—C and E radials; radial facets primitively plenary, peneplenary in derived forms, all similar on an individual; four to five primibrachials (one genus questionably assigned has one); more than ten arms.

Discussion.—Warn and Strimple (1977) described the Cincinnaticrinacea as containing one family and two subfamilies, and Guensburg (1984) added a third subfamily. As discussed above, the cincinnaticrinids are regarded as belonging to the order Homocrinida. These genera are still aligned as a single family, but subdivision into subfamilies is not considered necessary. Hence, the subfamilies Atopocrininae Warn and Strimple and Tryssocrininae Guensburg are synonymized with the Cincinnaticrinidae. *Columbicrinus* and *Praecursoricrinus* are reassigned to the Columbicrinidae, and *Othneiocrinus* is reassigned to the Atopocrinidae. *Glaucocrinus* is a poorly understood genus (Guensburg, 1992) and is questionably assigned to this family; it had previously been assigned to the Anomalocrinidae.

Included genera.—Arenig to Caradoc genera assigned to this family are *Cincinnaticrinus* Warn and Strimple, *Doliocrinus* Warn, *Isotomocrinus* Ulrich, *Ohiocrinus* Wachsmuth and Springer, *Tryssocrinus* Guensburg, and questionably *Glaucocrinus* Parks and Alcock. Additional younger taxa should also be assigned but those designations await further phylogenetic analyses.

Family ATOPOCRINIDAE Warn and Strimple, 1977

[*nom. transl.* Atopocrinidae Ausich, herein, *ex* Atopocrininae Warn and Strimple, 1977]

Diagnosis.—C and E radials; radial facets plenary and angustary on same individual; two or five primibrachials; ten pinnulate arms.

Discussion.—*Othneiocrinus* is a morphologically unusual crinoid that diverged early from *Ibexocrinus* but lacked descendants. This is regarded as a separate evolutionary event from the evolution of the cincinnaticrinids or the columbicrinids, so designation of a monogeneric family is necessary.

Included genus.—*Othneiocrinus* Lane.

Family COLUMBICRINIDAE new family

Diagnosis.—C and E radials; radial facets plenary, all same on an individual; one to three primibrachials; ten pinnulate arms.

Discussion.—The Columbicrinidae is designated for three Caradoc disparid crinoids that retained only the C and E radials and pinnulate arms. Based on phylogenetic analyses presented here, these three crinoids represent an independent lineage from *Isotomocrinus*.

Previously, *Columbicrinus* and *Praecursoricrinus* were assigned to the Cincinnaticrinidae, and *Geraocrinus* was assigned to the Anomalocrinidae.

Note that Guensburg (1984) synonymized *Praecursoricrinus* with *Columbicrinus*. Whereas this may indeed be the correct interpretation, the type species of these two genera differ in aboral cup shape, and the number of primibrachials and stem construction is variable. At least for the analyses presented here, these two genera are treated as distinctive.

Included genera.—*Columbicrinus* Ulrich, *Geraocrinus* Ulrich, and *Praecursoricrinus* Frest, Strimple, and McGinnis.

Order CALCEOCRINIDA new order

Diagnosis.—Disparids with aboral cup composed primitively of four lintels, five infrabasals, and three radials (B, C, and E rays), derived forms lose some lintels and radials; plate circlets articulated by a synarthrial ridge, asymmetrical about oral-aboral axis; aboral cup flattened or conical, radial facets peneplenary, and free arms branch.

Discussion.—The Calceocrinidae have previously been recognized as a distinctive lineage at the superfamilial level (Moore *et al.*, 1978). Here, the calceocrinids are elevated to an order because of the distinctiveness of morphology of these crinoids and the deeply rooted position of the Caradoc forms when analyzed with all other Arenig to Caradoc disparids (Fig. 6).

Included family.—Calceocrinidae Meek and Worthen.

Family CALCEOCRINIDAE Meek and Worthen, 1869

Diagnosis.—Same as for order.

Discussion.—Three middle Ordovician genera of this family exist, *Cremacrinus, Calceocrinus,* and *Paracremacrinus*. Harvey and Ausich (1997) interpreted the phylogeny of this family and agreed with Moore (1962) that *Cremacrinus* is the most primitive genus.

Included genera.—*Calceocrinus* Hall, *Anulocrinus* Ramsbottom, *Catatonocrinus* Brett, *Charactocrinus* Brett, *Chirocrinus* Angelin, *Chiropinna* Moore, *Cremacrinus* Ulrich, *Cunctocrinus* Kesling and Sigler, *Deltacrinus* Ulrich, *Diaphorocrinus* Eckert, *Dolerocrinus* Prick, *Eohalysiocrinus* Prokop, *Epihalysiocrinus* Arendt, *Espanocrinus* Webster, *Grypocrinus* Strimple, *Halysiocrinus* Ulrich, *Minicrinus* Prokop, *Paracremacrinus* Brower, *Senariocrinus* Schmidt, *Stibarocrinus* Ausich, *Synchirocrinus* Jaekel, and *Trypherocrinus* Ausich.

Order MYELODACTYLIDA new order

Diagnosis.—Disparids with aboral cup composed of five lintels, five infrabasals, and one radial (C ray); plate circlets symmetrical or asymmetrical about oral-aboral axis; aboral cup cone or bowl shaped, radial facets peneplenary or plenary, and free arms branch.

Discussion.—This order corresponds to the superfamily Myelodactylacea of Moore and Lane (1978d) without the Eustenocrinidae. Thus, this order is restricted to disparids with a single radial plate; one radial only in the C ray.

Included families.—Myelodactylidae S. A. Miller and Iocrinidae Moore and Laudon.

Family MYELODACTYLIDAE S. A. Miller, 1883

Discussion.—Details of this family not treated here.

Family IOCRINIDAE Moore and Laudon, 1943

Tornatilicrinidae Guensburg, 1984.

Diagnosis.—Myelodactylan with a large crown; crown erect on the column; numerous isotomous arm branches.

Discussion.—*Tornatilicrinus* is reassigned from Tornatilicrinidae Guensburg to the Iocrinidae, thus the former is a junior synonym of the latter.

Included genera.—*Iocrinus* Hall, *Caleidocrinus (Caleidocrinus)* Waagen and Jahn, *Caleidocrinus (Huxleyocrinus)* Donovan, *Pariocrinus* Rozhnov, 1988 (*non* Eckert, 1984), *Peltacrinus* Warn, and *Tornatilicrinus* Guensburg.

Order HYBOCRINIDA Jaekel, 1918

[*nom. transl. et correct.* Hybocrinida Moore, 1952, p. 613, *ex* suborder Hybocrinites Jaekel, 1918, p. 90]

Diagnosis.—Disparids with aboral cup composed of five lintels, five infrabasals, and one radial (C ray); plate circlets symmetrical about oral-aboral axis; aboral cup cone to globe shaped; radial facets angustary; free arms atomous.

Discussion.—Except for the removal of *Baerocrinus* and the Baerocrinidae, I follow herein the classification by Sprinkle and Moore (1978). Rozhnov (personal communication, 1996) considered *Baerocrinus* to be teratological.

Rozhnov (1985) argued that the hybocrinids should be elevated to subclass rank, equivalent to the Inadunata of Moore and Teichert (1978). Although the hybocrinids are morphologically distinct and unusual crinoids, this is not necessarily the case in the context of Early and middle Ordovician forms. During the initial crinoid radiation, a great disparity of morphologies developed that included, among others, the one-circlet ramseyocrinids, the calceocrinids with a hinged aboral cup, and the cleiocrinids with fused, hypertrophied brachials. In hybocrinids, the basic architecture is regarded as that of a disparid composed of five lintels, five infrabasals, and one radial plate, similar to iocrinids. Many of the seemingly unique features of hybocrinids represent either a lack of development or a reversal of characters to an ancestral condition, which is considered here to be that of rhombiferans (Ausich, 1996b, 1998b). On the basis of cryptic pentameres in *Hybocrinus nitidus* Sinclair, Sprinkle (1982) suggested the possibility that hybocrinids were pseudomonocyclic. Rozhnov (1985) used this condition as a criterion to designate the hybocrinids as a distinct subclass. If true, this would be strong evidence for separating the hybocrinids from the disparids. Ausich (1996), however, demonstrated that hybocrinids are similar to other disparids by considering the orientation of lumen angles, which was argued as the most reliable character for determining the symmetry relationship between the calyx and column.

Included families.—Hybocrinidae von Zittel, Hybocystitidae Jaekel, and Cornucrinidae Regnéll.

Family HYBOCRINIDAE von Zittel, 1879

Diagnosis.—Hybocrinids with five relatively short, erect arms; one in each ray.

Included genera.—*Hybocrinus* Billings, *Hoplocrinus* Grewingk, *Revalocrinus* Jaekel.

Family HYBOCYSTITIDAE Jaekel, 1918

Diagnosis.—Hybocrinids with three relatively short, erect arms with long, recurved ambulacral grooves in A, C, and D rays; two long, recumbent ambulacra, one each in B and E rays.

Included genus.—*Hybocystites* Wetherby.

Family CORNUCRINIDAE Regnéll, 1948

Diagnosis.—Hybocrinids with no erect arms; three recumbent arms, one each in A, C, and D rays; B and E ray with appendages or ambulacra absent.

Included genera.—*Cornucrinus* Regnéll and *Tripatocrinus* Sprinkle.

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Appendix A. Species from which morphological data were used to characterize genera for Arenig to Caradoc character analyses. Illustrations and descriptions of these species are by Moore and Teichert (1978) or can be located in the work of Bassler and Moodey (1943) or Webster (1973, 1977, 1986, 1988).

AETHOCRINIDS

Aethocrinus moorei Ubaghs (type species)
Perittocrinus radiatus (Beyrich) (type species)
Tetracionocrinus transitor (Jaekel) (type species)

CLADIDS

Agostocrinus xenus Kesling and Paul (type species)
Archaetaxocrinus burfordi Lewis (type species)
Carabocrinus huronensis Foerste (one of oldest species)
Colpodecrinus quadrifidus Sprinkle and Kolata (type species)
Compagicrinus fenestratus (Jobson and Paul) (type species)
Cupulocrinus humilis (Billings) (one of oldest species)
Dendrocrinus acutidactylus (Billings) (one of oldest species)
Elpasocrinus radiatus Sprinkle and Wahlman (type species)
Eoparisocrinus crossmani Brower (one of oldest species)
Eopinnacrinus pinnulatus Brower and Veinus (type species)
Esthonocrinus laevior Jaekel (type species)
Grenprisia billingsi Springer (type species)
Illemocrinus ampiatus Eckert (type species)
Merocrinus typus Walcott (type species)
Metabolocrinus rossicus Jaekel (type species)
Ottawacrinus typus Billings (type species)
for *Palaeocrinus* used two well-preserved species for determination of characters: *Palaeocrinus planobasalis* (Brower and Veinus) and *Palaeocrinus hudsoni* (Sinclair) new cladid genus and species (type species)
Plicodendrocrinus proboscidiatus (Billings) (one of oldest species)
Polycrinus ramulatus Jaekel (type species)
Porocrinus conicus Billings (type species)
Praecupulocrinus conjugans (Billings) (type species)
Quinquecaudex glabellus Brower and Veinus (type species)
Triboloporus cryptoplicatus Kesling and Paul (type species)
new cladid genus from Newfoundland Ausich, Bolton, and Cumming (1998)

FLEXIBLE

Protaxocrinus laevis (Billings) (one of oldest species)

CAMERATES

Abludoglyptocrinus laticostatus Kolata (one of oldest species)
Anthracocrinus primitivus Strimple and Watkins (type species)
Archaeocrinus lacunosus Billings (type species)
Balacrinus basalis (M'Coy) (type species)
Bromidocrinus nodosus Kolata (type species)
Celtocrinus ubaghsi Donovan and Cope (type species)
Cleiocrinus regius Billings (type species)
Cotylacrinna sandra Brower (type species)
Crinerocrinus parvicostatus Kolata (type species)
Deocrinus asperatus (Billings) (type species)
Diabolocrinus perplexus Wachsmuth and Springer (type species)
Eopatelliocrinus scyphogracilis Brower (type species)
Euptychocrinus skopaios (Shumard) (one of oldest species)
Glyptocrinus decadactylus Hall (type species)
Gustabilicrinus plektanikaulos Guensburg (type species)
Hercocrinus elegans Hudson (type species)
Neoarchaeocrinus pyriformis (Billings) (type species)
Paradiabolocrinus irregularis Brower and Veinus (type species)
Pararchaeocrinus decoratus Strimple and Watkins (type species)
Periglyptocrinus billingsi Wachsmuth and Springer (type species)
Proexenocrinus inyoensis Strimple and McGinnis (type species)
Pycnocrinus dyeri (Meek) (well-known species)
Reteocrinus alveolatus Miller and Gurley (one of oldest species)
Rhaphanocrinus sculptus (S. A. Miller) (well-known species)
Schizocrinus nodosus Hall (type species)
Simplocrinus persculptus Frest, Strimple, and Kelly (type species)
Trichinocrinus terranovicus Moore and Laudon (type species)

DISPARIDS

Acolocrinus hydraulicus Kesling and Paul (type species)
Apodasmocrinus daubei Warn and Strimple (type species)
Calceocrinus longifrons Brower (one of oldest species)
Caleidocrinus (*Caleidocrinus*) *multiramous* (Waagen and Jahn) (type species)
Caleidocrinus (*Huxleyocrinus*) *turgidulus* (Ramsbottom) (type species)
Cataraquicrinus elongatus Kolata (type species)
Cincinnaticrinus varibrachialus Warn and Strimple (type species)
Columbicrinus crassus Ulrich (type species)
Cornucrinus mirus Regnéll (type species)
Cremacrinus punctatus Ulrich (type species)
Daedalocrinus bellevillensis (W. R. Billings) (one of older species)
Difficilicrinus coneyi Frest, Strimple, and McGinnis (type species)
Doliocrinus pustulatus Warn (type species)
Ectenocrinus simplex Hall (type species)
Eustenocrinus springeri Ulrich (type species)
Geraocrinus sculptus Ulrich (type species)
Glaucocrinus falconeri Parks and Alcock (type species)
Hoplocrinus dipentas (Leuchtenberg) (type species)
Hybocrinus conicus Billings (type species)
Hybocystites problematicus Wetherby (type species)
Ibexocrinus lepton Lane (type species)
Inyocrinus strimplei Ausich (type species)
Iocrinus brithdirensis Bates (one of oldest species)
Isotomocrinus typus (type species)
Maennilicrinus concinnus Rozhnov (type species)
Ohiocrinus brauni Ulrich (well-known species)
Othneiocrinus priscus (Lane) (type species)
Pandoracrinus pinnulatus Jaekel (type species)
Paracremacrinus laticardinalis Brower (type species)
"*Pariocrinus*" *ladogensis* Rozhnov (type species)
Peltacrinus sculptatus Warn (type species)
Penicillicrinus parvus Warn (type species)
Peniculocrinus miller (Wetherby) (type species)
Pogonipocrinus antiquus Kelly and Ausich (type species)
Praecursoricrinus sulphurensis Frest, Strimple, and McGinnis (type species)
Pultivocrinus fundatus Rozhnov (type species)
Ramseyocrinus cambriensis (Hicks) (type species)
Revalocrinus costatus Jaekel (type species)
Ristnacrinus marinus Öpik (type species)
Tetragonocrinus pygmaeus (Eichwald) (type species)
Tornatilicrinus longicaudis Guensburg (type species)
Tripatocrinus pustulatus Sprinkle (type species)
Tryssocrinus endotomous Guensburg (type species)
Tunguskocrinus ivanovae Arendt (type species)
Virucrinus kegelensis (Yeltyscheva) (type species)
Vosekocrinus granulatus Jaekel (type species)

Appendix B. Characters, character states, and character matrix for Arenig to Caradoc cladids-flexibles for PAUP character analyses cited herein.

1. C radial smaller than others: 0, yes; 1, no
2. Radial facets: 0, fixed; 1, angustary; 2, peneplenary; 3, plenary; 4, fixed-recumbent
3. Number of infrabasal plates: 0, 5; 1, 4; 2, 3
4. Aboral cup shape: 0, medium cone; 1, medium globe; 2, low bowl; 3, low cone; 4, medium bowl; 5, high bowl
5. Radial circlet interrupted: 0, CD interray; 1, no interrays; 2, all
6. Basal concavity: 0, no; 1, yes
7. Pore rhombs: 0, no; 1, yes
8. Plate sculpturing (in addition to ray ridges, if present): 0, stellate; 1, smooth
9. Radianal in contact with: 0, infrabasals; 1, basals; 2, C radial; 3, lintels
10. Regular interradii with plate(s) in aboral cup: 0, yes; 1, at corners; 2, no
11. Brachials (most advanced state, typically most distal): 0, rectangular uniserial; 1, cuneate uniserial
12. Brachials fixed: 0, yes; 1, no
13. Erect arm number: 0, 5; 1, 0
14. Arm habit: 0, erect; 1, recumbent
15. Arm branching: 0, isotomous; 1, atomous; 2, endotomous ramules; 3, pinnulate; 4, heterotomous-recumbent; 5, isotomous-heterotomous
16. Number of primibrachials: 0, 7–11; 1, 1; 2, 2; 3, 3–6; 4, all
17. Patelloid processes: 0, no; 1, yes
18. Stem construction: 0, pentameric; 1, holomeric; 2, tetrameric
19. Columnal shape: 0, pentalobate; 1, circular; 2, pentagonal; 3, tetralobate
20. Lumen shape: 0, pentalobate; 1, circular; 2, pentagonal; 3, tetralobate
21. Column (based on proximal part): 0, heteromorphic; 1, xenomorphic; 2, homeomorphic

CHARACTER MATRIX FOR CLADIDS-FLEXIBLES.

Aethocrinus	00000	00000	00000	00000	0
Agostocrinus	14202	10032	00114	10022	?
Archaetaxocrinus	00000	00100	00005	300(12)0	0
Brechmocrinus	02000	00112	01000	00012	2
Carabocrinus	11040	01002	01000	20020	0
Colpodecrinus	00150	01010	00002	30233	0
Compagicrinus	01000	00002	01000	3000?	0
Cupulocrinus	03000	00111	01000	3(01)110	0
"*Dendrocrinus*"	01000	00112	01000	1011?	0
Elpasocrinus	01000	00002	01000	30011	0
Eoparisocrinus	01000	00012	01000	30(01)(12)0	0
Eopinnacrinus	02040	00112	11003	1011?	0
Esthonocrinus	01000	00012	01000	30?10	?
Grenprisia	01000	00111	01000	30021	0
Illemocrinus	01040	00012	01000	20(01)(12)0	0
Merocrinus	13031	00122	01000	30111	0
Metabolocrinus	03020	00012	11002	10110	0
Ontariocrinus	11000	00012	01000	2011?	0
Ottawacrinus	03000	00112	0100?	30022	0
Palaeocrinus	11010	01012	01000	(123)0010	0
Plicodendrocrinus	01000	00012	01005	30102 0	
Polycrinus	?3000	00112	01005	30?1?	0
Porocrinus	01010	01012	01001	40110	1
Praecupulocrinus	02030	00112	01000	(23)0112	1
Protaxocrinus	00200	00110	00000	21110	0
Quinquecaudex	02000	00110	0(01)000	30000	0
Triboloporus	11010	01012	0100?	30110	?

Appendix C. Characters, character states, and character matrix for Arenig to Caradoc camerates for PAUP character analyses cited herein.

1. Number of basal plates: 0, 5; 1, 3;
2. Number of infrabasal plates: 0, 5; 1, 0
3. Calyx shape: 0, medium cone; 1, high bowl; 2, low bowl; 3, low cone; 4, medium bowl; 5, high cone; 6, medium globe; 7, low globe
4. Radial circlet interrupted: 0, CD interray; 1, all interrays; 2, no interrays
5. Basal concavity: 0, no; 1, yes
6. Ray ridges: 0, yes; 1, no
7. Plate sculpturing (in addition to ray ridges, if present): 0, stellate; 1, smooth; 2, pustulose; 3, fine reticulate; 4, vermiform; 5, gently convex; 6, very convex; 7, knobby; 8, coarsely pitted; 9, ray ridges
8. Extra plates in CD interray: 0, yes; 1, no
9. Anitaxis of plates: 0, no; 1, yes
10. Anitaxial ridge: 0, no; 1, yes
11. Primanal in contact with: 0, CD basal; 1, C+D radials; 2, C radial
12. Posterior interradius plating: 0, iRA, sRA, X; 1, P-1-1; 2, P-3-3 or 2; 3, P-3-4 or 5; 4, X-P-3 or 2; 5, irregular; 6, P-1+-1+; 7, 2-3-3; 8, P-2-2
13. Interradial plating: 0, large plates; 1, small plates; 2, none
14. first primibrachial in contact with: 0, ibr1; 1, ibr 1+2; 2, ibr 2+3; 3, radial and ibr 1; 4, radial; 5, ibr 2; 6, ibr 4+5
15. Interradii plating (AB, BC, DE, EA): 0, I only; 1, I - 2; 2, I - 3; 3, ii - 3 or 4; 4, irregular; 5, none
16. Fixed pinnules: 0, no; 1, yes
17. Brachials (most advanced state, typically most distal): 0, rectangular uniserial; 1, cuneate uniserial; 2, biserial
18. Highest fixed brachials: 0, primibrachials; 1, secundibrachials; 2, tertibrachials; 3, quartibrachials; 4, sexibrachials
19. Intrabrachials: 0, no; 1, yes
20. Erect arm number: 0, 5; 1, 10; 2, 10–15; 3, 15–20; 4, 20; 5, 85–90
21. Arm branching: 0, isotomous; 1, atomous; 2, isotomous-heterotomous; 3, 1 isotomous
22. Free-arm character: 0, nonpinnulate; 1, pinnulate
23. Number of primibrachials: 0, 7–11; 1, 2; 2, 4–5
24. Stem construction: 0, pentameric; 1, holomeric
25. Columnal shape: 0, pentalobate; 1, circular; 2, pentagonal
26. Lumen shape: 0, pentalobate; 1, circular; 2, pentagonal; 3, complex pentalobate
27. Column (based on proximal part): 0, heteromorphic; 1, homeomorphic

CHARACTER MATRIX FOR CAMERATES

Abludoglyptocrinus	01400	02000	13011	11111	11111	?0
Aethocrinus	00000	00000	00000	00000	00000	00
Anthracocrinus	00011	03010	0(24)061	11313	11111	00
Archaeocrinus	00411	00010	030(41)1	02111	01111	00
Balacrinus	00610	01110	03002	11111	11111	10
Bromidocrinus	00611	04100	07023	02111	11100	00
Celtocrinus	015?0	00???	??011	00112	21111	?0
Cleiocrinus	00311	05010	012(40)5	01405	11102	21
Cotylacrinna	00211	06010	02011	12101	41101	00
Crinerocrinus	00711	00010	03022	0?214	??1??	??
Deocrinus	00611	17000	05014	11211	111?1	1?
Diabolocrinus	00211	10000	04051	02101	11111	00
Eopatelliocrinus	11020	00011	13011	11111	11111	00
Euptychocrinus	00000	05010	0301(12)	01111	11111	20
Glyptocrinus	01120	00011	12011	01214	11111	00
Gustabilicrinus	00411	11100	18011	11214	11111	20
Hercocrinus	00611	18100	05054	12101	?1111	20
Neoarchaeocrinus	00410	01???	0?011	02111	01111	00
Paradiabolocrinus	00711	00000	0?023	0?111	??1??	??
Pararchaeocrinus	00211	00011	24022	12111	01112	00
Periglyptocrinus	01120	00011	12011	02214	11111	10
Proexenocrinus	00411	09000	08011	01101	11111	?1
Pycnocrinus	01420	00011	12011	11111	01111	00
Reteocrinus	00410	09011	06164	00101	00201	30
Rhaphanocrinus	00410	000??	02021	00111	11111	10
Schizocrinus	01420	01???	1?011	01101	01211	20
Simplococrinus	00410	00000	03021	12214	111?1	??
Trichinocrinus	00311	19011	25001	01101	11112	20

Appendix D. Characters, character states, and character matrix for Arenig to Caradoc disparids for PAUP character analyses cited herein.

1. Radial plate in A ray: 0, yes; 1, no
2. Radial plate in B ray: 0, yes; 1, no
3. Radial plate in C ray: 0, yes; 1, no
4. Radial plate in D ray: 0, yes; 1, no
5. Radial plate in E ray: 0, yes; 1, no
6. Radial or infrabasal facets: 0, fixed; 1, angustary; 2, peneplenary; 3, plenary; 4, multiple small; 5, none
7. Articulation between lintels and infrabasals: 0, absent; 1, present
8. Number of infrabasal plates: 0, 5; 1, 4; 2, 3; 3, 0
9. Number of lintels: 0, 5; 1, 4; 2, 3; 3, 0
10. Aboral cup shape: 0, medium cone; 1, cylindrical; 2, low cone; 3, medium bowl; 4, high cone; 5, medium globe
11. Radial circlet interrupted: 0, yes; 1, no
12. Basal concavity: 0, no; 1, yes
13. Lintels visible: 0, yes; 1, no
14. Anal X in contact with: 0, CD basal; 1, C+D infrabasal; 2, C radial; 3, primibrachial 1; 4, none
15. Posterior interradius plating: 0, iRA, sRA, X; 1, X only; 2, none
16. Respiratory structure: 0, no; 1, yes
17. Brachials (most advanced state): 0, rectangular uniserial; 1, cuneate uniserial; 2, none
18. Erect arm number: 0, 5; 1, 4; 2, 3; 3, 0; 4, 40+
19. Arm habit: 0, erect; 1, recumbent
20. Recumbent arm number: 0, 0; 1, 2; 2, 3
21. Arm branching: 0, isotomous; 1, atomous; 2, none; 3, 1 isotomous-pinnulate; 4, endotomous pinnulation; 5, endotomous ramulate; 6, bilateral heterotomy; 7, 1 isotomous-ramulate; 8, 1 isotomous-heterotomous
22. Brachials fixed between adjacent proximal rays: 0, no; 1, yes
23. Number of primibrachials: 0, 7–11; 1, 1; 2, 2; 3, 3; 4, 4–6; 5, >11; 6, all; 7, none
24. Stem construction: 0, pentameric; 1, holomeric; 2, tetrameric; 3, trimeric
25. Columnal shape: 0, pentalobate; 1, circular; 2, pentagonal; 3, tetralobate; 4, tetragonal
26. lumen shape: 0, pentalobate; 1, circular; 2, pentagonal; 3, tetralobate; 4, tetragonal; 5, elliptical
27. Column (based on proximal part): 0, heteromorphic; 1, homeomorphic; 2, xenomorphic
28. Proximal anal on D radial: 0, yes; 1, no.
29. Lintel cirlet width to height ratio: 0, 2.2 to 2.8; 1, 1.1 to 2.0; 3, 0.5; 4, 3.0 to 5.0.
30. Secundibrachial number: 0, many; 1, 4–5; 2, 2–3; 3, all; 4, none.
31. Aboral cup higher than wide: 0, no; 1, yes.

CHARACTER MATRIX FOR DISPARIDS

Acolocrinus	00000	40023	01011	11400	10611	?1014	0
Apodasmocrinus	10010	30003	10021	01000	7020(01)	00002	0
Calceocrinus	10110	21011	11022	00000	00211	21102	0
Caleidocrinus (C.)	11011	20002	10122	00000	0021(12)	12131	0
Caleidocrinus (H.)	11011	10003	10021	00000	0021(12)	12132	0
Cataraquicrinus	10010	30000	10021	00000	00(04)02	0001?	0
Cincinnaticrinus	11010	30000	10021	00000	70402	22011	1
Columbicrinus	11010	30003	10021	01000	30(23)(01)(12)	00013	0
Cornucrinus	11011	50010	100?2	02312	20711	01124	0
Cremacrinus	10010	21011	11021	00100	60211	20102	0
Daedalocrinus	10010	30002	10021	00000	50(34)00	00012	0
Difficilicrinus	10110	30002	10011	0?000	???00	0?03?	0
Doliocrinus	11010	30000	10021	0?000	?0?01	20011	0
Ectenocrinus	10010	30000	10021	01000	70231	00012	1
Eustenocrinus	00000	30000	10022	00100	01001	20110	1
Geraocrinus	11010	(23)0002	10021	00000	40(12)01	00003	0
Glaucocrinus	11010	10003	10021	00000	70100	10102	0
Hoplocrinus	11011	10003	10011	00000	10611	0?014	0
Hybocrinus	11011	10000	10011	00000	10611	01014	0
Hybocystites	11011	10005	10011	002(01)3	10611	01034	0
Ibexocrinus	10010	30000	10021	00000	80(0234)01	01000	1
Inyocrinus	00000	20000	?00??	00000	00011	?1?00	0
Iocrinus	11011	30000	10022	00000	00(04)1(12)	20110	0
Isotomocrinus	11010	30000	10021	00000	00402	20010	0
Maennilicrinus	11111	20004	10022	00000	004??	??113	0
Ohiocrinus	11010	30000	10021	00000	80412	?0001	0
Othneiocrinus	11010	(23)0000	10032	01000	30(24)01	2?103	0
Paracremacrinus	11110	21011	11021	01100	60211	?0132	0
"*Pariocrinus*"	11011	20000	10022	00000	00301	20110	1
Peltacrinus	11011	20000	10021	00000	00(234)00	20131	0
Penicillicrinus	10010	30000	10021	00000	002?1	?0011	0
Peniculocrinus	00000	30000	10032	00000	01(04)12	2000?	1
Pogonipocrinus	00000	30000	?00??	00000	00212	?0?00	0
Praecursoricrinus	11010	30000	10021	01000	3021(12)	00013	0
Pultivocrinus	11111	30000	10022	0?000	?0???	??11?	0
Ramseyocrinus	11111	30012	1?142	00000	00523	3010?	1
Revalocrinus	11011	10000	10022	00000	?0???	??0??	?
Ristnacrinus	00000	30030	10021	00000	01(12)11	500?1	0
Tetragonocrinus	11111	30312	10042	00200	00(234)24	4011?	1
Tornatilicrinus	11011	30000	10021	00000	7000(12)	20100	0
Tripatocrinus	11011	50005	00001	02312	107??	??014	0
Tryssocrinus	11010	?0000	00011	00000	714(01)(01)	00012	1
Tunguskocrinus	10010	30003	10021	00000	001?1	1?013	0
Virucrinus	10000	30100	10021	00100	0000(01)	20113	1
Vosekocrinus	11111	10003	?00??	00000	002?0	??132	0