MORPHOLOGY OF ORDOVICIAN - DEVONIAN CRINOIDS

BY

MIKE FOOTE

CONTRIBUTIONS FROM THE MUSEUM OF PALEONTOLOGY

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Abstract—This paper presents a set of discrete characters to quantify morphology in Ordovician-Devonian crinoids and to allow documentation of temporal patterns of morphological diversity (disparity). The characters cover skeletal form broadly, and represent four principal regions of the skeleton: the pelma (14 characters); the dorsal cup (26 characters); the arms, fixed brachials and interbrachials (27 characters); and the anus and tegmen (8 characters). Analysis of character data for a large sample of Ordovician-Devonian species reveals that, although taxonomic diversity increased from the Ordovician to the Lower Devonian, disparity for the Ordovician-Devonian interval had attained its maximal level by the mid Ordovician (early Caradocian). In agreement with previous work, the data presented here suggest that certain limits to crinoid form were reached after an initial burst of morphological diversification.

INTRODUCTION

Macroevolutionary patterns of morphological diversity, or *disparity*, have provided important clues to smaller-scale evolutionary processes within clades (e.g., Saunders and Swan, 1984; Campbell and Marshall, 1987; Gould, 1989; Briggs et al., 1992; Foote, 1993a). However, if we are to determine which large-scale patterns, and by inference which lower-level mechanisms, predominate in the history of life, many more clades need to be studied. As a monophyletic group with a rich and varied array of forms, a skeleton that reflects soft anatomy and functional morphology well, a long history showing several phases of diversification, and a good fossil record, the Crinoidea represent a nearly ideal group in which to document the evolution of morphological disparity.

This paper will describe a set of discrete characters with which to quantify crinoid morphology, and then present morphological data for a large sample of species representing

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the clade's diversification during the Ordovician, Silurian and Devonian. The data will be used to demonstrate that high morphological disparity was attained early at relatively low taxonomic diversity, and that disparity did not increase after the Ordovician despite substantial taxonomic diversification. More detailed analyses and interpretations are presented in a companion paper (Foote, 1994). Briefly, the patterns of disparity and diversity suggest that, after an initial period of substantial morphological diversification, some basic limits to crinoid form must have been reached. Evidently, subsequent taxonomic diversification involved relatively minor variations on the major designs that were established early (Ausich, 1988).

MATERIALS AND METHODS

Quantifying Crinoid Form.—Although certain groups of crinoids are stable enough in their skeletal design to allow a morphometric approach involving continuous characters (e.g., David C. Kendrick's work on Flexibilia, pers. comm., June 23, 1993), the class as a whole is so variable in basic plate number and arrangement that an adequate set of measures of overall morphology is difficult to construct. Growth has been extensively measured (e.g., Macurda, 1968; Brower, 1973, 1987), paleoecological inferences have been drawn from measurement of ecologically significant features (e.g., Lane, 1963b; Ausich, 1980; Brower, 1987, 1992), and the form of calyces has been modeled (Kendrick, 1993). Variability in crinoid form has been addressed by recognizing a number of morphotypes or calyx designs (e.g., Springer, 1926, Brower, 1973, Ausich, 1988). To expand on the last approach and to increase resolution, I have used a set of discrete (mostly binary) characters to describe crinoid form. Characters, listed in Table 1, were chosen to represent the major regions of the crinoid skeleton that are generally well preserved. Although the characters include many that are taxonomically useful at various levels and many that are of known functional significance, presumed taxonomic or functional relevance were not used as grounds for character choice. Rather, broad coverage and overall description of the crinoid skeleton were the goals.

In contrast to some previous work that focused on the acquisition of novelties (e.g., Derstler, 1982), this study is concerned with overall morphological disparity and, therefore, considers both primitive and derived character states in quantifying morphology (Briggs et al., 1992; Foote, 1992b; Wills et al., 1994). I have emphasized characters that can be coded on most or all crinoids. The rationale behind this approach is to keep comparison among species as meaningful as reasonably possible without sacrificing too much information (i.e., to keep the number of "no-comparison" character states as low as reasonably possible). Among the crinoids sampled, the average number of inapplicable characters per species (for example, presence or absence of arm branching in forms lacking arms) was about 12 out of 75 characters, or about 16%. The characters reflect a compromise between precision and generality (Raup, 1966, 1967; Cherry et al., 1982), which is necessary when considering the entire class Crinoidea with a single set of characters. Studies of smaller groups of crinoids have often involved much finer detail (e.g., Lane, 1963a; Brower, 1973, 1982, 1988; Macurda, 1974; Webster, 1981; Kammer and Ausich, 1992, 1993). An initial set of 107 characters was considered, but many of these were omitted from analysis because they proved to be invariant, apparently redundant with other characters, or too difficult to code reliably. A total of 75 characters was used: 14 pertaining to the pelma, 26 pertaining to the dorsal cup, 27 pertaining to the arms (including fixed brachial and interbrachial plates), and 8 pertaining to the anus and tegmen. The character set for the arms resembles the scheme that Kendrick (1992) used to consider all crinoid arms in a common morphological space. Characters are presented in more detail in Table 1 and Appendix 1.

Character coding was based mainly on illustrated descriptions of species from the primary literature, and in a few cases on examination of museum specimens (see Appendices 2 and 3 for data and literature sources). Species that are too poorly preserved, described, or illustrated

to allow reliable coding of most characters were omitted. I coded missing characters as unknown rather than relying on authors' guesses or assuming that such characters had the same states as in related species.

Extensive homeomorphy has long been recognized as a major feature of crinoid evolution (e.g., Moore and Laudon, 1943; Brower, 1973; Broadhead, 1988a,b; Ausich, 1988; Kammer and Ausich, 1992). In coding characters to assess morphological disparity, rather than phylogenetic uniqueness, it is crucial that character states be defined so that forms that have converged with respect to a particular character be considered identical with respect to that character (Foote, 1992b). For example, stems that consist of a series of alternating larger and smaller columnals are all considered to occupy effectively the same locus in morphospace with respect to character 3 (absence or presence of a heteromorphic stem), and are therefore coded identically for this character.

The approach to character coding relies on the arrangement of plates rather than their inferred evolutionary origin, which is sometimes rather uncertain (e.g., Kelly, 1982, Broadhead, 1988a,b). For example, evolutionary sequences suggest that the plate commonly referred to as the radianal in Cladida and Flexibilia is homologous whether it forms an inferradial plate in the C ray or an anal plate in the CD interray (Moore, 1962; Ubaghs, 1978). This plate is coded differently depending on its position. When it is in the interradial position it is coded as an anal plate and the C-radial is coded as simple. When it is clearly in the C-radial position, it is coded as an inferradial and the C-radial is coded as compound, just as in many members of the Disparida. At one level, a disparid inferradial and a cladid-flexible radianal in the inferradial position represent different characters (i.e., they are apparently not homologous). However, at the scale of analysis employed here they do represent topologically convergent features. This emphasis on plate arrangement is not meant to suggest that detailed evolutionary pathways are unimportant, only that they pertain to a different set of questions than those addressed here. When quantifying morphological disparity, we must emphasize the net array of realized forms, and their similarities and differences, regardless of the detailed pathways by which that array was realized (Gould, 1991). This approach may seem odd to those who employ discrete-character data for phylogenetic inference, but it is in principle the same approach as used in other investigations of morphospace occupation. For example, if we use coiling parameters to study ammonoid form (Raup, 1966, 1967), two species with the same whorl expansion rate are not inferred necessarily to be closely related but rather to be morphologically similar.

Because disparity measures the magnitude of differences among species, not the direction of those differences, character polarity (primitive versus derived) is not considered explicitly. A species with a pentameric stem and one with a holomeric stem would differ from each other morphologically to the same degree whether pentameric or holomeric stems were primitive.

Sampling.—In contrast to phylogenetic analysis, certain species are not considered "key" taxa when measuring disparity. Rather, a representative sample is required. Two main goals guided the sampling of species for this study: (1) to obtain a reasonably large and broadly representative sample of species for each stratigraphic interval; and (2) to keep the number of unknown character states as low as reasonably possible by omitting poorly preserved or inadequately described species. To some extent these two goals are at odds, but a comparison between generic richness and sample size for several higher taxa suggests that the representation of the major crinoid clades and grades is generally proportional to their known taxonomic diversity (Table 2). Moreover, nearly half (48%) of all known Ordovician-Devonian genera are represented by morphological data in this study.

A list of publications was compiled from a number of bibliographic sources (including Webster, 1969, 1977, 1986, 1988, Moore and Teichert, 1978, and the *Zoological Record*), and these publications were searched for descriptions of crinoid species. Generic taxonomy seems more stable than taxonomy at the species level (see Kammer and Ausich, 1992). In order to

TABLE 1— Characters used to quantify crinoid form. Characters are denoted as binary (B), ordered multistate (O), or unordered multistate (U). The coding of characters is meant to describe overall form in a consistent way, rather than to identify strict homology. No polarity of characters is implied by coding.

Character	Character description and states

Pelma

1(U)   Pelma: 0, absent. 1, multiplated holdfast. 2, column. 3, single massive plate forming 'peduncle.'

2(B)   Column strongly xenomorphic: 0, no. 1, yes.

3(B)   Form of proximal column: 0, apparently homeomorphic. 1, visibly heteromorphic.

4(B)   Form of proximal column: 0, not coiled. 1, coiled.

5(B)   Form of proximal columnals: 0, holomeric or cryptomeric. 1, visibly meric.

6(U)   Shape of proximal columnals: 0, (sub)circular. 1, (sub)elliptical. 2, trigonal. 3, trilobate or tristellate. 4, tetragonal. 5, tetralobate or tetrastellate. 6, pentagonal. 7, pentalobate or pentastellate.

7(U)   Lumen shape of proximal columnals: same states as character 6.

8(B)   Relative height of proximal columnals: 0, discoid (H/W < 0.5). 1, elongate (H/W ≥ 0.5).

9(B)   Proximal columnal articulation: 0, synostosis or cryptosymplexy. 1, symplexy.

10(B) Cirri in proximal part of column: 0, absent. 1, present.

11(B) Cirral arrangement (proximal): 0, irregular. 1, regular.

12(B) Cirral arrangement (proximal) (if regular): 0, columns. 1, whorls.

13(B) Specialized distal structure: 0, absent. 1, present.

14(U) Form of distal structure: 0, irregular plates (stellar holdfast). 1, radix. 2, discoidal holdfast, float, or other. 3, encrustation.

Dorsal cup

15(B) Plating: 0, irregular. 1, regular.

16(O) Number of radials: state = count.

17(B) Radial circlet closed or open: 0, closed. 1, open.

18(U) Nature of opening: 1, anal interray only, open by anals. 2, anal interray only, open by basals. 3, open in anal and/or other interrays.

19(B) Number of circlets between radial and basal-most: 0, zero (monocyclic). 1, one (dicyclic).

20(B) Radial prongs or sinus: 0, absent. 1, present.

21(B) Relative development of radials: 0, (sub)equal. 1, unequal.

22(B) Compound radials: 0, absent. 1, present.

23(O) Number of compound radials, if present: state = count.

24(O) Relative size of radial circlet area: 0, less than about half basalmost circlet area. 1, subequal with basalmost circlet area. 2, greater than about twice basalmost circlet area.

25(O) Number of plates in basalmost circlet: state = count.

26(B) Relative development of plates in basalmost circlet (if more than one plate): 0, (sub)equal. 1, unequal.

27(B) Intermediate circlet open or closed: 0, closed. 1, open.

28(U) Nature of opening: 1, anal interray only, open by anals. 2, anal interray only, open by radials. 3, open in anal and/or other interrays.

29(O) Number of plates in intermediate circlet: state = count.

30(B) Relative development of plates in intermediate circlet: 0, (sub)equal. 1, unequal.

31(O) Relative size of intermediate circlet area: 0, less than about half radial circlet area. 1, subequal with radial circlet area. 2, greater than about twice radial circlet area.

32(O) Number of anal plates in cup at or below level of radials: 0, zero. 1, one. 2, two. 3, three or more.

33(U)   Shape of cup (sag.): 0, cylinder. 1, cone. 2, bowl. 3, globe. 4, irregular.
34(O)   Shape of cup (sag.): 0, low (W/H > 1.5). 1, medium. 2, high (H/W > 1.5).
35(U)   Shape of cup (trans.): 0, round. 1, polygonal or convex. 2, lobate or stellate.
36(U)   Symmetry of cup (trans.): 0, asymmetric. 1, strongly bilateral. 2, triradial. 4, tetraradial. 5, pentaradial with strong bilateral overprint. 6, pentaradial (with or without weak bilateral overprint). [Note: There is no state 3.]
37(B)   Shape of base: 0, convex or flat. 1, concave.
38(B)   Maximal diameter of cup relative to stem diameter: 0, < 2.5. 1, ≥ 2.5.
39(B)   Median ray ridges on cup: 0, absent. 1, present.
40(B)   Stellate ridges on cup plates: 0, absent. 1, present.

Arms
41(B)   Presence of arms: 0, absent. 1, present.
42(O)   Number of distinct arms: state = count.
43(O)   Maximal number of arms directly attached to single radial: 0, one. 1, two. 2, more than two.
44(O)   Relative development of arms: 0, (sub)equal. 1, slightly unequal. 2, strongly unequal.
45(O)   Predominant separation of arms at cup: 0, appressed or nearly so. 1, less than about 1.5 arm widths apart. 2, greater than about 1.5 arm widths apart.
46(B)   Visible lateral arm fusion between rays: 0, absent. 1, present.
47(B)   Arm branching distal to point where distinct: 0, unbranched. 1, branched.
48(O)   Effective number of orders of branching: 0, one. 1, two. 2, three or more.
49(B)   Arm branching: 0, mainly isotomous. 1, mainly heterotomous.
50(U)   Predominant form of heterotomy: 0, bilateral. 1, endotomous. 2, exotomous. 3, other regular (e.g., abradial or adradial). 4, irregular.
51(B)   Arm plating: 0, characteristically uniserial. 1, characteristically biserial.
52(B)   Patelloid process (if uniserial): 0, absent. 1, present.
53(B)   Brachial shape (if uniserial): 0, symmetric. 1, cuneate, asymmetric.
54(O)   Brachial shape (H/W): 0, < 0.5. 1, 0.5-1.0. 2, 1.0-2.0. 3, > 2.0.
55(B)   Visible lateral fusion of free arm plates within ray: 0, absent. 1, present.
56(O)   Predominant arm attitude: 1, sloping inward, vertical, or forming cone. 2, sidewards. 3, pendent.
57(B)   Recumbent arms: 0, absent. 1, present.
58(B)   Incorporation of (radially aligned) brachial plates into cup: 0, no. 1, yes.
59(O)   Extent of brachial incorporation into cup (number of ranges): state = count.
60(B)   Interbrachials (including fixed pinnules) in cup: 0, absent. 1, present.
61(B)   Form of proximal interbrachials: 0, small, irregular. 1, larger, regular.
62(B)   Pinnules: 0, absent. 1, present.
63(O)   Characteristic maximal number of pinnules per brachial: state = count.
64(B)   Recumbent ambulacra on cup: 0, absent. 1, present.
65(O)   Number of recumbent ambulacra: state = count.
66(B)   Predominant extent of recumbent ambulacra: 0, less than halfway down cup. 1, halfway or more.
67(O)   Ratio of arm length to cup height: 0, <1. 1, 1-2. 2, 2-4. 3, >4.

Anal and tegminal features
68(B)   Anal opening through dorsal cup: 0, no. 1, yes.
69(B)   Anal tube or sac: 0, no. 1, yes.
70(O)   Predominant position of tube or sac: 0, posterior. 1, (sub)central. 2, anterior.
71(B)   Extent of tube or sac relative to cup height: 0, ≤2. 1, >2.
72(B)   Ridges (including plicae) on proximal part of tube or sac: 0, no. 1, yes.
73(B)   Plating of tube or sac: 0, at least partly regular. 1, irregular.
74(B)   Development of tegmen (other than tube/sac): 0, orals only or a few large plates. 1, multiplated.
75(B)   Extent of tegmen (other than tube/sac) relative to cup height: 0, ≤2. 1, >2.

TABLE 2— Time scale, crinoid generic richness, and sample sizes. Ages (Ma) and durations (m.y.) from Harland et al. (1990). Number of genera from Foote (1994). Total generic richness includes genera of unknown affinities, and so is greater than sum of genera within listed higher taxa for some intervals. Numbers in parentheses show the numbers of species that would be expected if the number of species sampled for each higher taxon, relative to the total number of species sampled in that interval, were equivalent to the number of genera known within each higher taxon, relative to the total number of genera known in that interval.

Stratigraphic interval	Age (base)	Dura-tion	Diplo-bathrida	Mono-bathrida	Hybo-crinida	Dispar-ida	Clad-ida	Flexi-bilia	Total
				Number of genera					
Lower Ordovician (LO)	510	34	1	1	1	9	2	--	14
Ordovician-2 (O2)	476	18	19	2	4	25	11	1	72
Ordovician-3 (O3)	458	19	14	10	4	21	16	2	67
Llandoverian (L)	439	9	14	27	--	13	8	3	65
Wenlockian (W)	430	6	10	33	--	16	22	21	102
Upper Silurian (US)	424	15	11	29	--	18	19	8	95
Lower Devonian (LD)	409	23	16	43	--	21	39	12	135
Middle Devonian (MD)	386	9	15	28	--	24	45	14	126
Upper Devonian (UD)	377	15	3	9	--	6	29	10	57
				Number of species sampled					
Lower Ordovician (LO)	510	34	1 (0.3)	0 (0.3)	0 (0.3)	1 (2.6)	2 (0.6)	--	4
Ordovician-2 (O2)	476	18	8 (9.8)	2 (1.0)	1 (2.1)	14(12.9)	6 (5.7)	1 (0.5)	32
Ordovician-3 (O3)	458	19	5 (6.5)	8 (4.6)	2 (1.9)	9 (9.7)	6 (7.4)	1 (0.9)	31
Llandoverian (L)	439	9	4 (4.1)	4 (7.9)	--	6 (3.8)	3 (2.3)	2 (0.9)	19
Wenlockian (W)	430	6	1 (4.1)	7(13.6)	--	8 (6.6)	11 (9.1)	15 (8.6)	42
Upper Silurian (US)	424	15	5 (2.8)	8 (7.3)	--	4 (4.5)	2 (4.8)	5 (4.5)	24
Lower Devonian (LD)	409	23	7 (5.3)	11(14.1)	--	5 (6.9)	17(12.8)	3 (3.9)	43
Middle Devonian (MD)	386	9	4 (5.0)	12 (9.3)	--	5 (8.0)	14(15.0)	7 (4.7)	42
Upper Devonian (UD)	377	15	1 (0.9)	2 (2.8)	--	1 (1.9)	11 (9.2)	3 (3.2)	18

reduce the effects of variation in species concepts and to keep the study tractable, I have allowed each genus to be represented by no more than one species within any of the nine stratigraphic intervals used for this study. Morphological variation within a genus is small relative to that within crinoids as a whole (Foote, 1994; see also Kammer and Ausich, 1992 who discuss the stability of discrete characters at the generic level). Therefore, restricting sampling in this way probably has little effect on large-scale patterns of disparity. Although isolated columns and columnals have aided our understanding of crinoid evolution, particularly the early evolution of the class (Donovan, 1986, 1989a,b), it is prudent for present purposes to represent species by their overall form. I have therefore omitted species that are known only from their columns. [After this study was completed, I discovered that two species of the genus *Macrostylocrinus* were inadvertently included in the Ordovician-3 sample, as were two species of *Deltacrinus* in the Middle Devonian. These oversights have virtually no effect on the results. The average dissimilarity (see below) among Ordovician-3 species is equal to 0.234 when only one species is retained, compared with 0.233 when both are retained. For the Middle Devonian the corresponding figures are 0.232 and 0.235. In both cases, including a duplicate species within a genus leads to a difference in disparity that is small compared to the standard error of disparity measures (Fig. 1).]
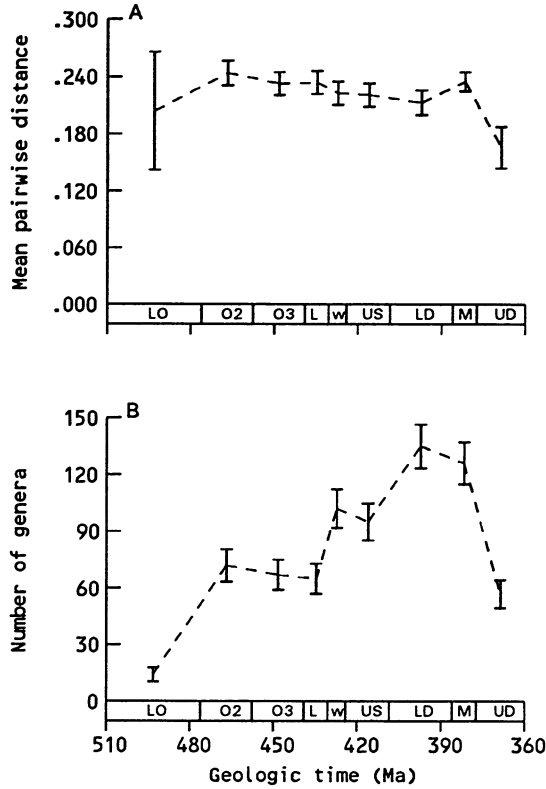
FIG. 1—Temporal sequence of morphological disparity and taxonomic diversity in Ordovician through Devonian crinoids. A. Mean pairwise dissimilarity between species. Error bars are based on bootstrap resampling (Efron, 1982) of data with 200 replicates, and show one standard error on either side of disparity estimate. Because species are phylogenetically related, and therefore do not represent independent data points (Raup and Gould, 1974; Felsenstein, 1985), standard errors are best thought of as providing some estimate of analytical error, i.e. the variability in results that might be expected if sampling and analysis of species were repeated a number of times (see Foote, 1993b). B. Generic diversity, showing the total number of known genera (not the number sampled for morphological data) (data from Foote, 1994). Error bars estimated as $\pm \sqrt{D}$, where D is the number of genera; this estimate is an approximation of the counting error used by Sepkoski and Raup (1986). Note that morphological disparity increases to its maximal level by Ordovician-2, at relatively low taxonomic diversity, and does not subsequently increase despite a substantial increase in taxonomic diversity. Abbreviations for stratigraphic intervals as in Table 2.

Stratigraphic Intervals and Resolution.—The Ordovician, Silurian, and Devonian were divided into nine stratigraphic intervals reflecting a compromise between resolution and sample size (Table 2). These intervals are: (1) Lower Ordovician (Tremadocian-Arenigian; roughly Ibexian and Whiterockian through zone N); (2) Ordovician-2 (Llanvirnian, Llandeilian, and lower part of Caradocian, i.e. through the North American Blackriveran); (3) Ordovician-3 (remainder of Caradocian plus Ashgillian, i.e. Rocklandian through Gamachian); (4) Llandoverian; (5) Wenlockian; (6) Upper Silurian (Ludlovian plus Pridolian); (7) Lower Devonian (Lochkovian, Pragian, and Emsian); (8) Middle Devonian (Eifelian and Givetian); and (9) Upper Devonian (Frasnian and Famennian). Variance in interval length apparently has a relatively minor effect on large-scale temporal patterns in the data (Foote, 1994).

RESULTS

Diversity versus Disparity.—Mean pairwise dissimilarity among species provides a measure of disparity that is intuitively reasonable and unbiased by sample size (Cherry et al., 1982; Foote, 1991, 1992a,b, 1993a,b). In practice there is little difference whether the mean or median dissimilarity is used. The dissimilarity between two species is measured as the total character difference divided by the number of characters compared (Sneath and Sokal, 1973). For any given species, some characters may be unknown and some logically inapplicable; therefore, the total number of characters compared between two species is generally less than 75. Because total character difference is divided by the number of characters compared, missing or inapplicable characters do not generally bias between-species distances. The average character distance between two species (not its square root, which is sometimes employed; Sneath and Sokal, 1973) is comparable to a squared distance based on continuous morphometric characters. Therefore, the mean pairwise distance for a sample of species is comparable to a sample variance (Van Valen, 1974). For binary characters and most unordered multistate characters, the character difference is equal to zero if the two species have the same character state and unity if their character states differ. In order to allow equal weighting of characters, ordered multistate characters were scaled so that the maximal character difference for each character is unity. See Appendix 1 for further discussion of character states and the calculation of character differences.

Taxonomic diversity increased from the Lower Ordovician through the Lower Devonian, while disparity reached its maximal Ordovician-Devonian level by the early part of the Caradocian (Fig. 1). Certain patterns of diversity and disparity may be masked by the coarse level of stratigraphic resolution. For example, the slight drop in disparity between Ordovician-2 and the Llandoverian may be underlain by a larger drop followed by an increase (see Foote, 1994).

Extremes in Morphospace.—Because an increase in disparity (i.e., mean dissimilarity) would be expected in an evolving system without morphological boundaries (i.e., in a case of unbounded diffusion) (Stanley, 1973; Fisher, 1986; Gould, 1988; Foote, 1993a), the foregoing result suggests the possibility that some morphological boundaries were reached during the Ordovician. However, approximate stasis in disparity still allows the possibility that the entire distribution of crinoid form may have shifted without expanding. Figures 2 and 3, which represent a continuous ordination of species along principal-coordinate axes derived from the between-species distances (Gower, 1966), suggest that this was generally not the case. Average morphology is not quite static; but for most of the principal-coordinate axes, fluctuations or trends in the mean are small if we compare them to the range of forms present in Ordovician-2 and if we consider that these changes occurred over more than 100 million years. Clearly, the extreme forms in the Ordovician-2 sample are not the most extreme forms represented in the entire Ordovician-Devonian interval. However, given that there are over 200 species sampled after Ordovician-2, some expansion of sampled extremes is to be expected even if the underlying distribution of forms did not change at all. Application of extreme-value statistics (Gumbel, 1958) shows that the extent to which Ordovician-2 extremes are surpassed exceeds the expectation of sampling alone for some, but not most, principal-coordinate axes (Foote, 1994).

Character Combinations.—Given discrete character data, an intuitive notion of disparity lies in the number of unique combinations of character states exhibited by a sample of species. However, this concept of disparity has two shortcomings. First, like the extent of morphospace occupation, the number of character-state combinations is strongly biased by sample size (Foote, 1992a). Second, as the number of characters increases, the number of potential

combinations becomes astronomical. Therefore, the number of unique character-state combinations is about the same as the number of species and provides more information on taxonomic diversity than on disparity.

In an important study considering a great variety of animal skeletons in a common character space, Thomas and Reif (1993) circumvented the second problem by considering characters two at a time, thus projecting the multidimensional character space onto a series of planes, each defined by a pair of character axes. Figure 4 shows the Thomas-Reif graph for all Ordovician-Devonian crinoids sampled, as well as the Middle Cambrian *Echmatocrinus* (Sprinkle, 1973), which is questionably assigned to the Crinoidea (see Conway Morris, 1993; Simms and Sevastopulo, 1993). Each main division of the axes represents a character, and the subdivisions represent character states of this character. The numbers in parentheses along the diagonal give the number of character states for each character. To simplify the graph, several characters were recoded to have fewer states, as explained in the legend. Black cells in the graph indicate character-state combinations that are known to occur in the sample of species. White cells indicate combinations that are not known to occur. Because the sample of species is necessarily incomplete, and because some character data are unknown, white cells cannot be interpreted to indicate true absence of a character-state combination. Finally, cells filled with an × indicate character-state combinations that are logically impossible. For example, consider characters 33 (shape of cup; four states) and 37 (shape of base; two states). The intersection of these two characters on the graph shows that all eight cells are filled; cylindrical cups, conical cups, bowl-shaped cups, and globe-shaped cups each are known in species having convex bases and concave bases. Looking at characters 40 (presence or absence of stellate ridges) and 41 (presence or absence of arms), we see that all cells but one are occupied; the sole sampled species that lacks arms also lacks stellate ridges on its cup plates. Character 41 also illustrates a set of illogical character-state combinations; if arms are lacking, characters 42-67, pertaining to the arms, cannot be coded.

Given that over 70% of all cells in Figure 4 are filled, it might appear as though crinoid character space was quite richly occupied. This is somewhat misleading, because invariant characters were omitted from analysis. Nevertheless, the occupation of the space can be used to ask whether the overall spectrum of crinoid form attained during the Ordovician-Devonian had essentially been reached by the Middle Ordovician. Because the number of occupied cells depends strongly on sample size, even if all samples of crinoids are drawn from the same spectrum of forms, it is appropriate to compare the number of character-state combinations for Ordovician-2 crinoids to the number we might reasonably expect for a sample from the entire set of crinoids. Rarefaction of number of character-state combinations against number of species (Fig. 5) shows that the diversity of form in Ordovician-2 crinoids is well within what we would expect if Ordovician-2 forms were sampled at random from the gross distribution. This does not imply that all *particular* character-state combinations were present in the Ordovician, only that the *number* of them was not unusually small. It is difficult to make a case for a persistent, temporal increase in morphological disparity.

Distribution of Suprageneric Taxa in Principal-Coordinate Space.—When the discrete character data are converted to an ordination using principal-coordinates analysis, some separation of the major higher taxa is achieved (Fig. 6; Foote, 1994). This is to be expected, since many of the characters are known to be useful in discriminating the higher taxa (subclasses and orders) (Moore et al., 1978; Foote, 1994). Distributions of species within finer subdivisions of these higher taxa are shown in Figures 7-11. The classification used here is primarily that of Moore et al. (1978). Not all the taxa are generally believed to represent clades. In evaluating these distributions, it should be borne in mind that an ordination in only a few dimensions inevitably distorts distances between species based on multidimensional data. Therefore, the relative distances between particular species in Figures 6-11 may not accurately reflect their relative dissimilarities based on all the character data.
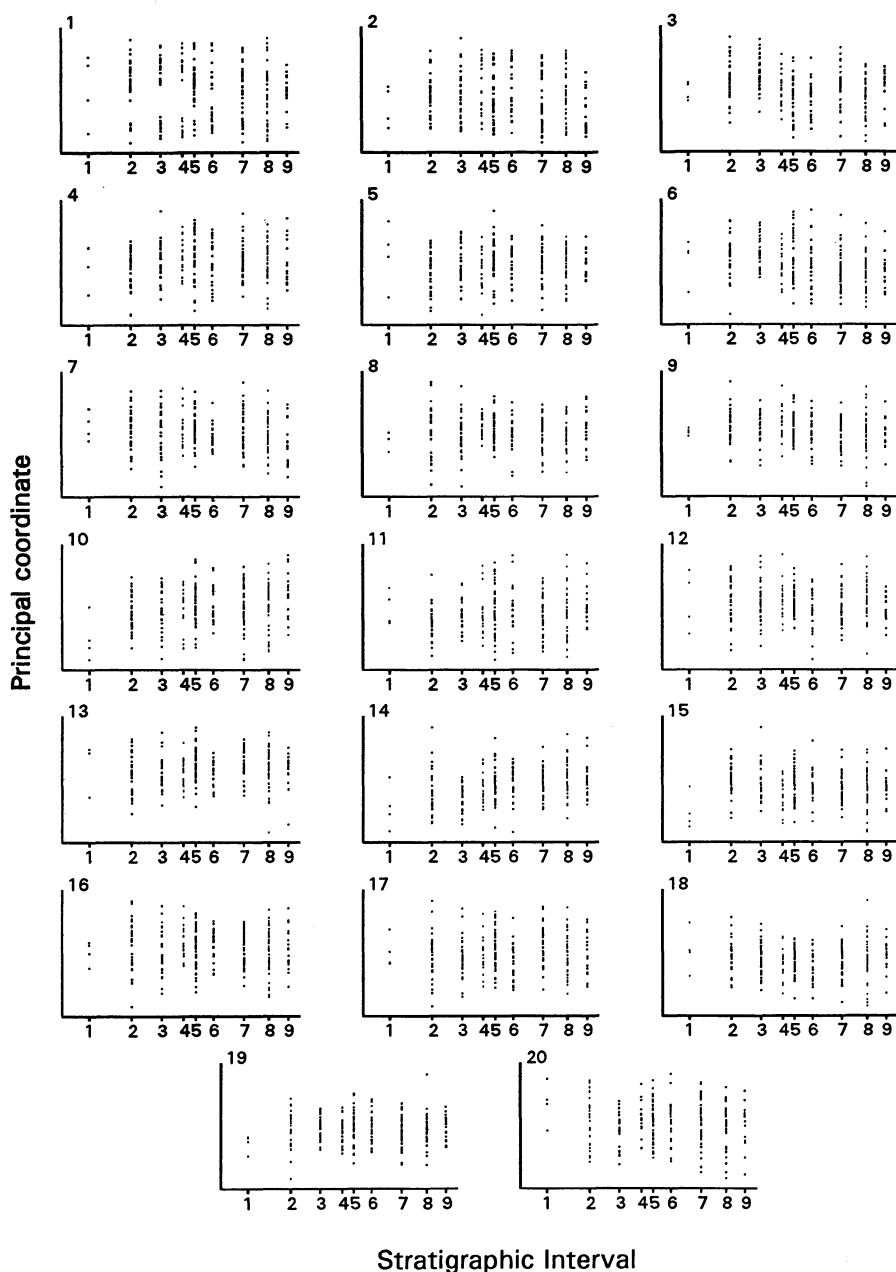
FIG. 2—Distributions of crinoids along first twenty principal-coordinate axes. Because there are missing data, the method of principal coordinates (rather than principal components analysis) is used to obtain an ordination directly from the distances between species (Gower, 1966). The number of axes examined is somewhat arbitrary, reflecting a compromise between information retention and manageability (see Foote, 1994). Each point represents a species. The overall impression given by the distributions along most axes is that, relative to the range of forms present in the Lower Ordovician and Ordovician-2 (intervals 1 and 2 in this figure), the distributions do not shift substantially after Ordovician-2, nor do the observed minima and maxima expand substantially. See Foote (1994) for analysis of observed minima and maxima.
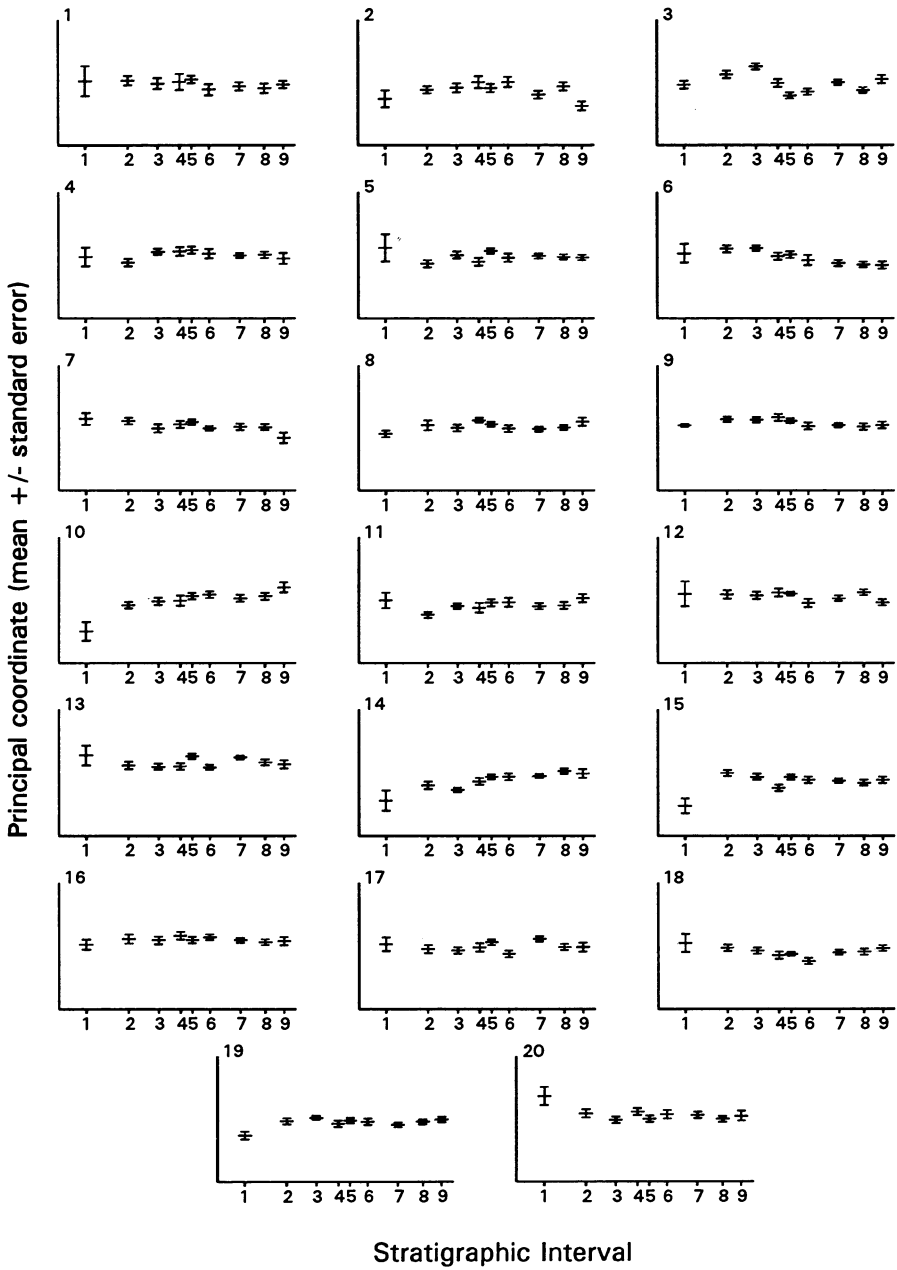
FIG. 3—Temporal sequence of means (± one standard error) along first twenty principal-coordinate axes. This figure is plotted at the same scale as Fig. 2. Note that, although the means fluctuate or shift along some axes, these changes in mean form are mostly small compared to the range of forms present in the Lower Ordovician and Ordovician-2. The temporal sequence is too short to allow reasonable statistical testing for trends, but note that only along axes 10, 13, and 14 are six or more of the eight changes in the same direction.
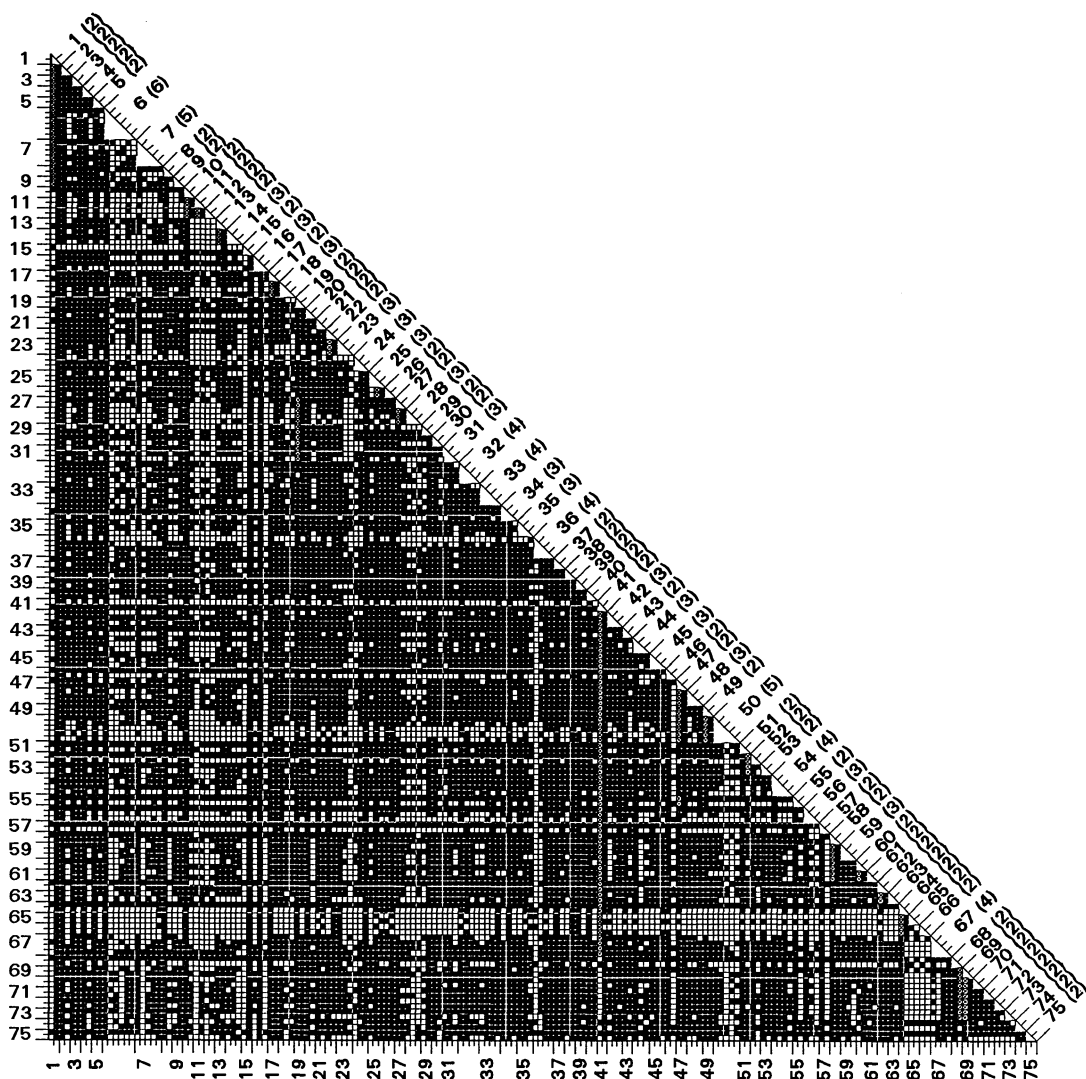
FIG. 4—Thomas-Reif graph showing realized character-state combinations for all crinoids studied. Major, numbered divisions along vertical, horizontal, and diagonal axes refer to characters in Appendix 1. Only odd-numbered characters are labelled on vertical and horizontal axes. Numbers in parentheses along diagonal give the total number of character states present. Minor divisions indicate different character states. Black cells indicate that the character-state combination is present in the data. White cells indicate that the character-state combination, while feasible, is not present in the data. Cells marked with an × indicate character state combinations that are not logically possible (for example, number of arms if arms are not present). Over 70% of cells are filled, but this high proportion partly reflects omission of invariant characters. Character states are in the same order as listed in Appendix 1, with the exception of the following characters: (1) (character 1) only two states (1 and 2) are shown in figure, because states 0 and 3 are not present in the data; (2) (character 6) only six states (0, 1, 4, 5, 6, and 7) are shown, because states 2 and 3 are not present in the data; (3) (character 7) only five states (0, 4, 5, 6, and 7) are shown, because states 1, 2, and 3 are not →
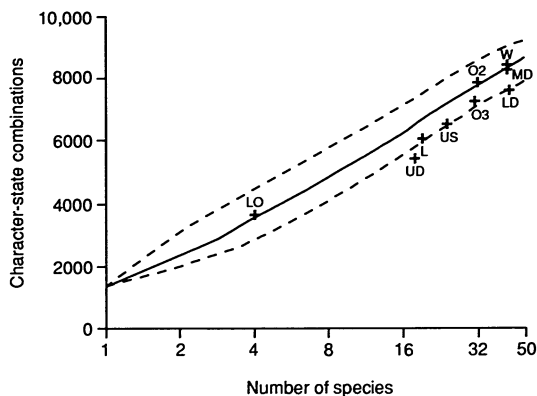
FIG. 5—Rarefaction of number of realized character-state combinations against number of species sampled (on a logarithmic scale). The solid curve gives the number of character-state combinations to be expected in a subsample of species drawn from the entire sample of 256 species (255 Ordovician-Devonian species and *Echmatocrinus brachiatus* from the Middle Cambrian [Sprinkle, 1973]). The dashed curves show the approximate 90% confidence interval for this expectation (see Foote, 1992a for rarefaction procedure). Labelled points show the number of species sampled and the number of character-state combinations realized for the nine Ordovician-Devonian stratigraphic intervals (abbreviations as in Table 2). Rarefaction suggests that the number of character-state combinations in the Ordovician-2 sample is not less than would be expected if Ordovician-2 forms were representative of crinoids as a whole.

present in the data; (4) (character 14) only three states (1, 2, and 3) are shown, because state 0 is not present in the data; (5) (character 16) character is recoded to have three states, corresponding to fewer than five radials, five radials, and more than five radials; (6) (character 23) character is recoded to have three states, corresponding to one compound radial, between two and four compound radials, and five or more compound radials; (7) (character 25) character is recoded to have three states, corresponding to one plate, between two and four plates, and five or more plates; (8) (character 29) character is recoded to have two states, corresponding to fewer than five plates, and five or more plates; (9) (character 36) only four states (0, 1, 5, and 6) are shown, because states 2 and 4 are not present in data; (10) (character 42) character is recoded to have three states, corresponding to fewer than five arms, five arms, and more than five arms; (11) (character 43) character states 1 and 2 are combined; (12) (character 59) character is recoded to have three states, corresponding to one or two ranges of fixed brachials, three to ten ranges, and greater than ten ranges; (13) (character 63) character is recoded to have two states, corresponding to a single pinnule per brachial, and two or more pinnules per brachial (hyperpinnulate); (14) (character 65) the two character states correspond to three and four recumbent ambulacra, respectively; (15) (character 70) only two character states (0 and 1) are shown, because character state 2 is not present in the data.
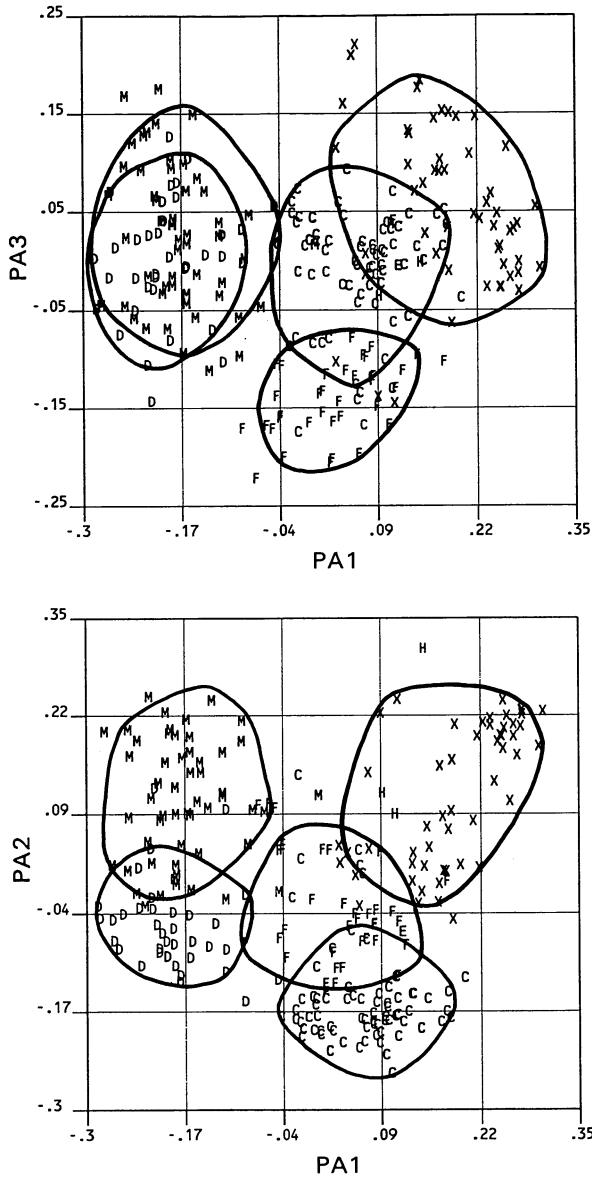
FIG. 6—Distributions of Ordovician-Devonian crinoid species, plus the Middle Cambrian *Echmatocrinus*
(Sprinkle, 1973), along first three principal-coordinate axes (PA). Although missing data prevent
precise calculation of the proportion of information in the original data contained in these three
principal coordinates, the sum of the first three eigenvalues of the Gower-transformed distance matrix
divided by the total sum of eigenvalues is equal to 42%. Solid lines show the envelopes containing
90% of the species lying closest to the group centroid (based only on the plotted axes for each
bivariate graph) for Diplobathrida, Monobathrida, Flexibilia, Cladida, and Disparida. By omitting the
most extreme species for each group, these envelopes are intended to give an idea of the morphological
field occupied by the majority of species within each higher taxon. No envelope is drawn for
Hybocrinida, for which only three species were sampled. The hybocrinid near the top of the bottom
figure is the abrachiate *Cornucrinus*. Note that the representation of morphology allows a fair
separation among the principal higher taxa of crinoids. Key to taxa: C, Cladida; D, Diplobathrida,
E, *Echmatocrinus*; F, Flexibilia; H, Hybocrinida; M, Monobathrida; X, Disparida.
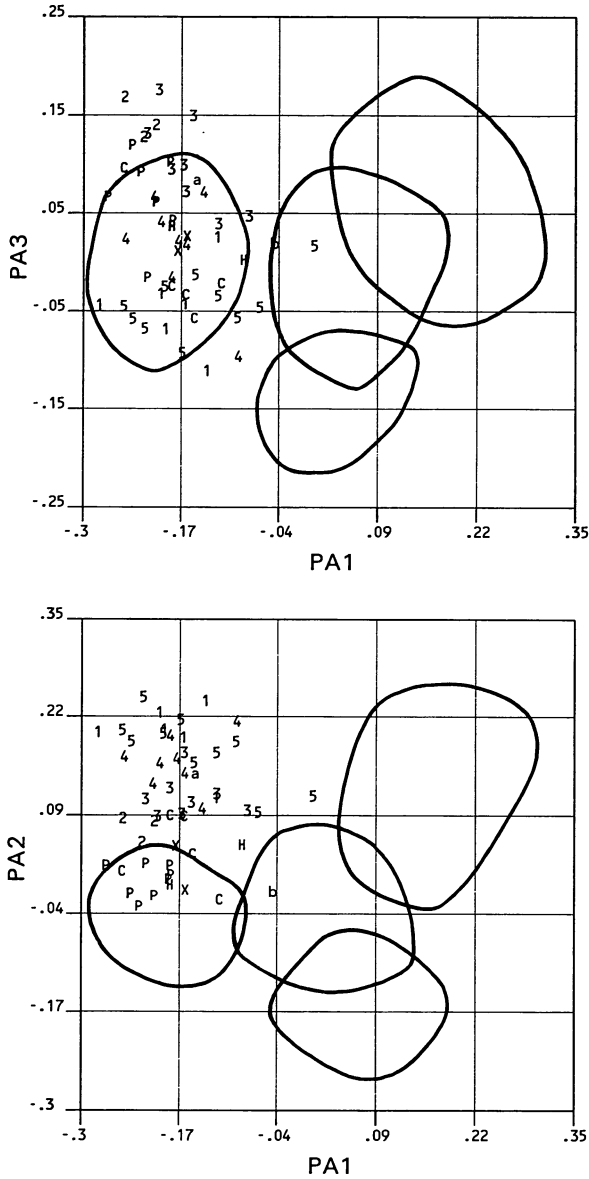
FIG. 7—Species of Monobathrida along first three principal-coordinate axes. In this and subsequent figures, the envelope of the higher taxon of interest is omitted, but envelopes of the other taxa are included for comparison. Key: upper case letters, Compsocrinina (C, Carpocrinacea; H, Hexacrinitacea; P, Periechocrinacea; X, Xenocrinacea); numerals, Glyptocrinina (1, Eucalyptocrinitacea; 2, Glyptocrinacea; 3, Melocrinitacea; 4, Patelliocrinacea; 5, Platycrinitacea); a, *Stipatocrinus*; b, *Colpodecrinus*. Note that the orders Glyptocrinina and Compsocrinina occupy different morphological fields, but the same is not so clearly the case for superfamilies within these orders.
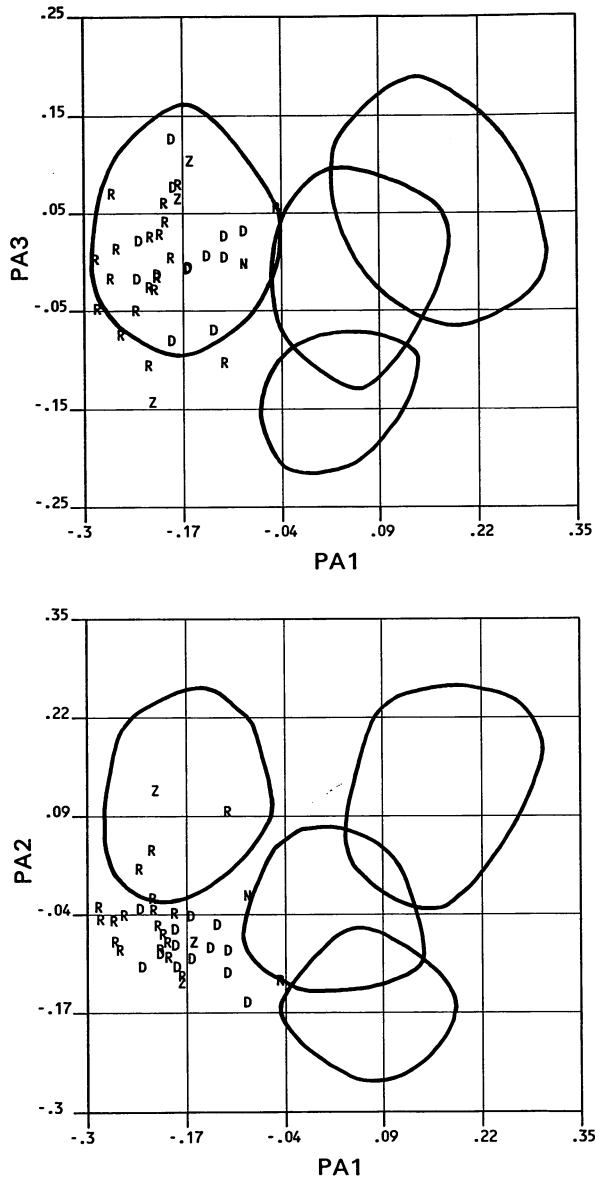
FIG. 8—Species of Diplobathrida along first three principal-coordinate axes. Key: D, Dimerocrinitacea; N, Nyctocrinacea; R, Rhodocrinitacea; Z, Zygodiplobathrina. Dimerocrinitacea and Rhodocrinitacea occupy largely different fields along the first axis.
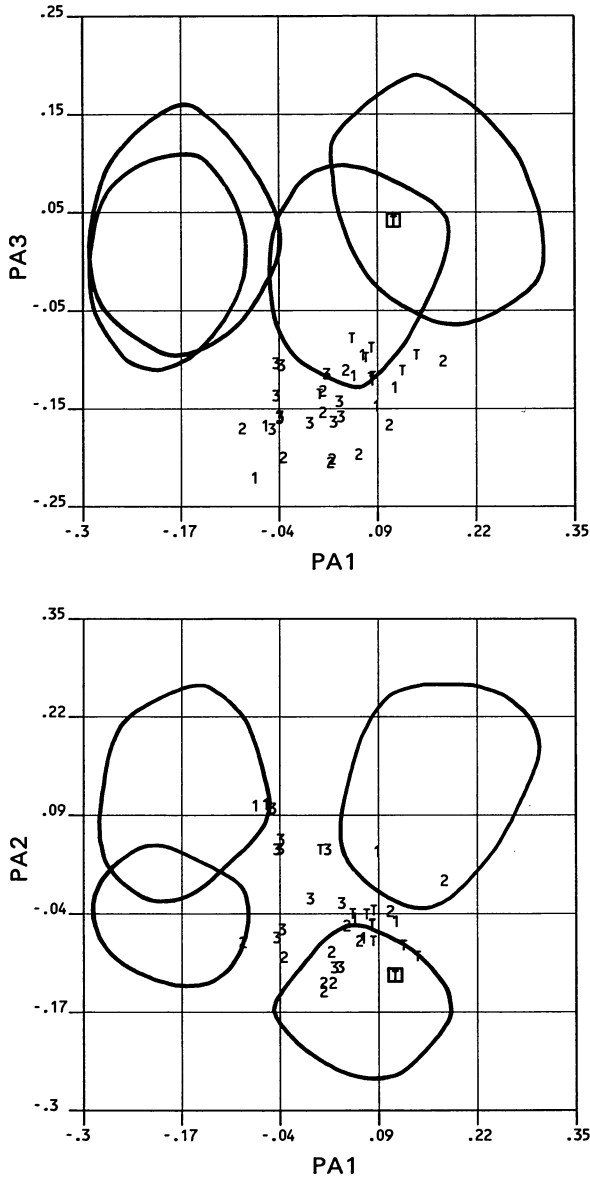
FIG. 9—Species of Flexibilia along first three principal-coordinate axes. Key: numerals, Sagenocrinida (1, Icthyocrinacea; 2, Lecanocrinacea; 3, Sagenocrinitacea); T, Taxocrinida (including *Archaeotaxocrinus*). *Archaeotaxocrinus*, indicated by a T within a box, falls within the cladid field, near *Cupulocrinus*, to which it is believed to be related (Lewis, 1981; see also Springer, 1920; cf. Fig. 10 herein). Sagenocrinids appear more dispersed than taxocrinids. Sagenocrinids also overlap with the morphological fields of all other higher taxa depicted here.
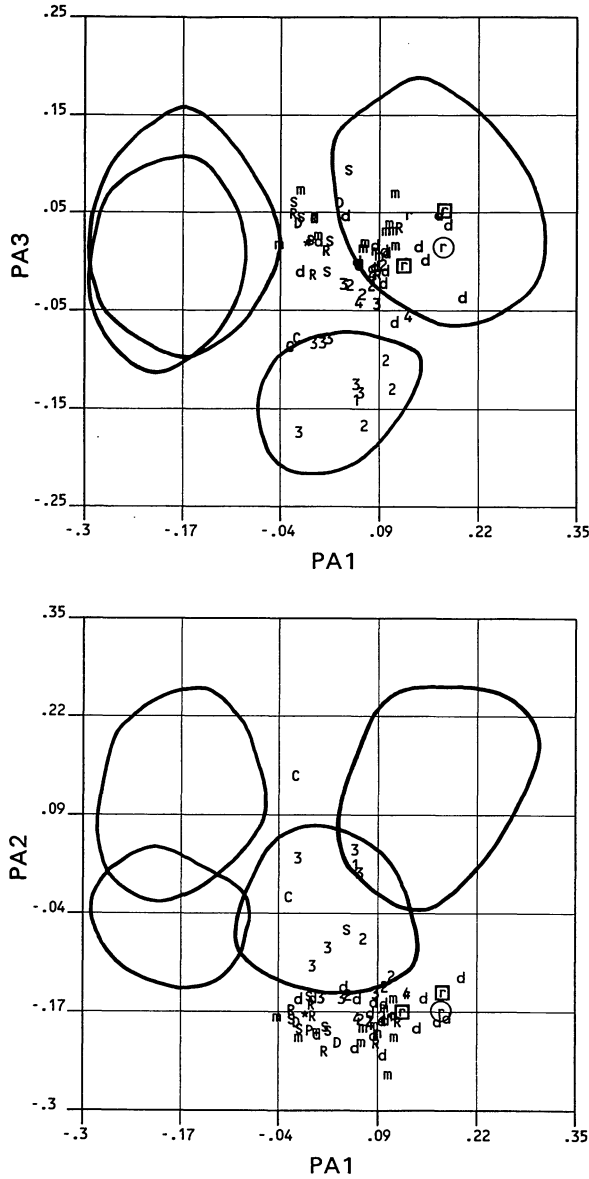
FIG. 10—Species of Cladida along first three principal-coordinate axes. Key: numerals, Cyathocrinina (1, Codiacrinacea; 2, Cyathocrinitacea; 3, Gasterocomacea; 4, Thalamocrinidae [*Thalamocrinus*, *Illemocrinus*, and *Kanabinocrinus*]); lower case letters, Dendrocrinina (d, Dendrocrinacea; m, Mastigocrinacea; r, Merocrinacea); upper case letters, Poteriocrinina (C, Cupressocrinitacea; D, Decadocrinacea; P, Poteriocrinitacea; R, Rhenocrinacea; S, Scytalocrinacea); *, *Idaeumocrinus*. For comparison with *Archaeotaxocrinus* in Figure 9, two species of *Cupulocrinus* are marked by an r within a box, and one species of *Praecupulocrinus* by an r within a circle. Note that Cyathocrinina overlaps considerably with morphological field of Flexibilia, and that Dendrocrinina and Poteriocrinina appear to overlap with each other more than either does with Cyathocrinina.
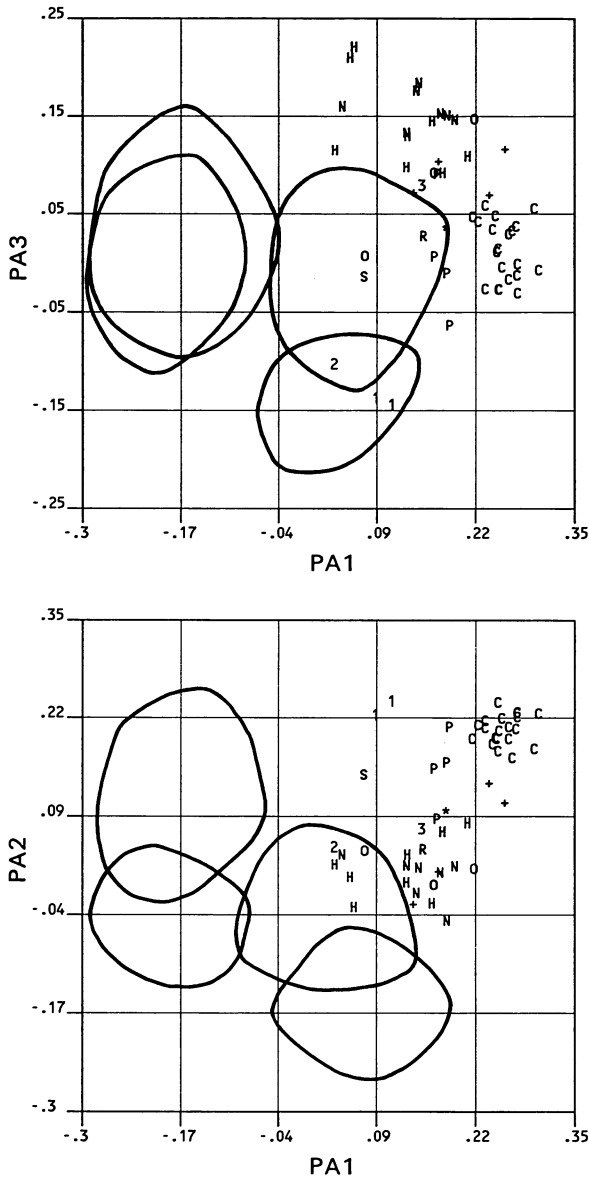
FIG. 11—Species of Disparida along first three principal-coordinate axes. Key: numerals, Allagecrinacea (1, Acolocrinidae; 2, *Agostocrinus*; 3, Anamesocrinidae); C, Calceocrinidae (Calceocrinacea); H, Homocrinidae (Homocrinacea); N, Cincinnaticrinidae (Cincinnaticrinacea); P, Pisocrinidae (Pisocrinacea); S, Sybathocrinidae (Belemnocrinacea); R, *Ramseyocrinus*; other symbols, Myelodactylacea (*, Eustenocrinidae; O, Iocrinidae; +, Myelodactylidae).

A few salient features in Figures 7-11 should be noted. Within Monobathrida, the suborders Compsocrinina and Glyptocrinina are generally separate along the second principal-coordinate axis, but the superfamilies within these suborders are not as easily discriminated (Fig. 7). Within Diplobathrida, the superfamilies Rhodocrinitacea and Dimerocrinitacea are relatively distinct along the first principal-coordinate axis (Fig. 8). Within Flexibilia, the order Taxocrinida seems to be less dispersed than the order Sagenocrinida (Fig. 9). This would be expected from even a cursory glance at the variety of sagenocrinid forms (Springer, 1920). Flexible crinoids, particularly Sagenocrinida, overlap with the morphological fields of Monobathrida, Diplobathrida, Cladida, and Disparida. The oldest flexible, *Archaeotaxocrinus* (here included with Taxocrinida), lies within the cladid field, not far from *Cupulocrinus*, with which the flexibles probably share a close relationship (e.g., Springer, 1920; Lewis, 1981; cf. Fig. 10 herein). Within Cladida, the suborders Dendrocrinina and Poteriocrinina appear to overlap with each other more extensively than either does with Cyathocrinina, which itself extends considerably into the morphological field of flexibles (Fig. 10). Within Disparida, the superfamilies Homocrinacea and Cincinnaticrinacea overlap considerably, while Calceocrinacea is quite distinct (Fig. 11). Bilateral symmetry in crinoids is perhaps most strongly developed in calceocrinids. It is noteworthy that some members of Pisocrinidae and Myelodactylidae, in which bilateral symmetry is somewhat more weakly but still conspicuously developed, lie near the morphological field of calceocrinids.

Effect of character weighting.—As discussed in Appendix 1, the perceived pattern of morphological disparity inevitably depends to some extent on the choice of characters. Character complexes for which more characters are coded are implicitly given more weight (e.g., the cup with 26 characters *vs.* the stalk with 14 characters). Analysis of three subsets of characters corresponding to the stalk, cup, and arms, respectively, reveals no pronounced tendency for disparity within any character set to increase after the mid Ordovician (Foote, 1994). The same holds when characters that are important for discriminating the major higher taxa are omitted (Foote, 1994). These results suggest that the major temporal pattern—a lack of increase in disparity despite substantial taxonomic diversification—is not an artifact of character choice.

Once characters are chosen, however, results depend to some extent on how the characters are weighted. Without a justifiable scheme for differential weighting, all characters have been weighted equally. One can gain some idea of the effect of weighting by assigning weights at random (Fig. 12). If the failure of morphological disparity to increase (Fig. 1) were very sensitive to character weighting, we would expect at least some sets of arbitrarily assigned weights to yield an increasing trend in disparity. That numerous sets of randomly assigned weights yield no such result suggests that the relative stability in morphological disparity is quite robust, and is not an artifact of equal weighting of characters.

DISCUSSION

Analysis of discrete characters has been used to suggest that morphological disparity in Ordovician-Devonian crinoids reached its maximal level by the Middle Ordovician. Because a continued increase in disparity is expected in a diversifying clade that has not reached its morphological boundaries, this result suggests that some limits to crinoid form were reached relatively early. Further study of post-Devonian crinoids (in progress) should help reveal just how strict these limits may have been. Discrete characters with a few states have built-in limits. However, the results presented here and elsewhere (Foote, 1994; see also Ausich, 1988) are based not on single characters but on overall patterns of character variation and covariation and on combinations of multiple characters. Thus, the observed temporal pattern of disparity is unlikely to be an artifact of the use of discrete characters with a limited number
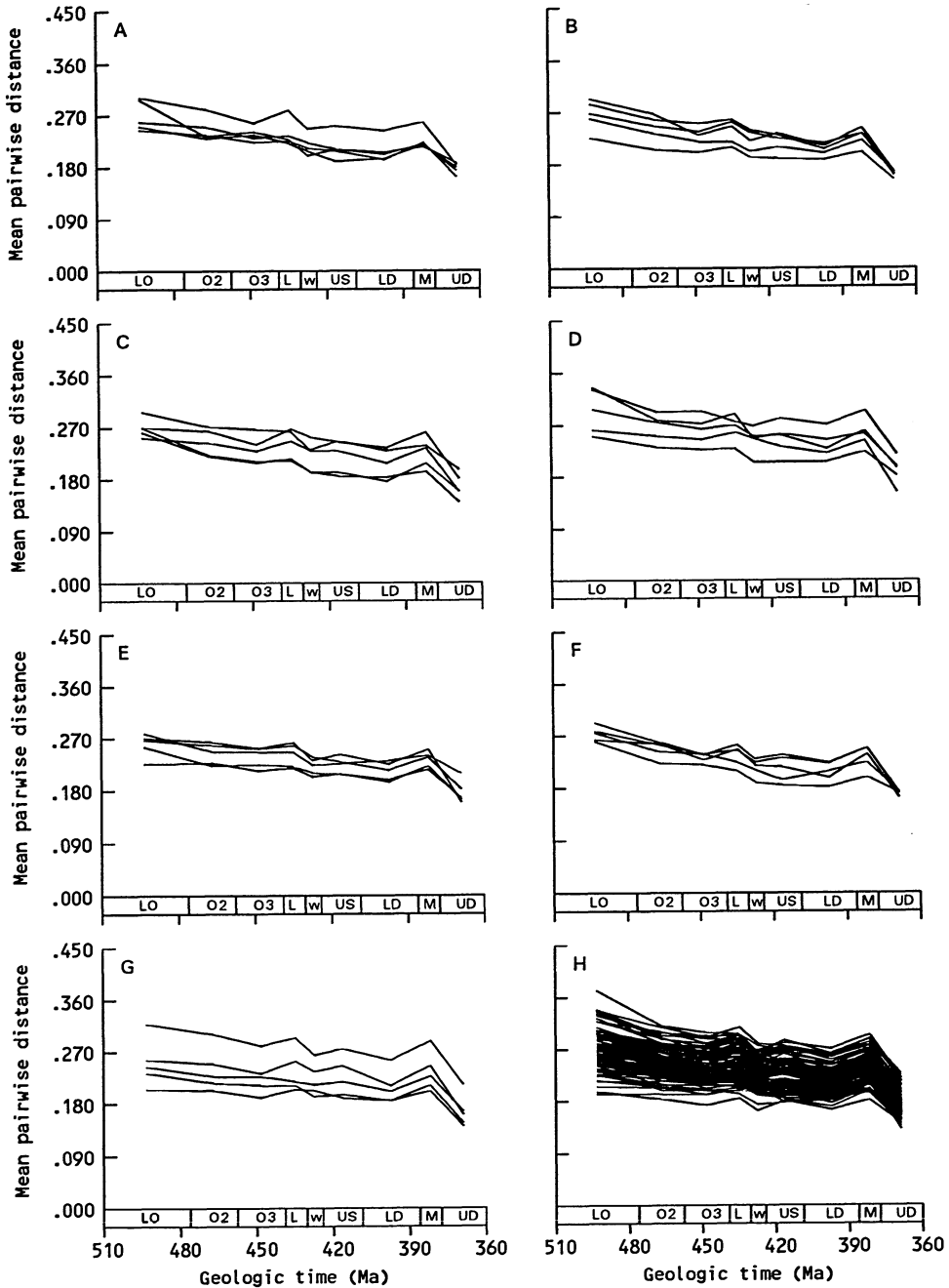
FIG. 12—Time series of morphological disparity with randomly assigned character weights. For each time series, each character is assigned a weight uniform on (0,2). Weights could have been assigned on any interval, but assigning them on (0,2) yields an average weight of unity over a large number of time series, thus facilitating comparison with Fig. 1. Panels A-G each show only five different time series, so that each trajectory can be followed clearly. Panel H shows 100 time series. Randomly assigned character weights do not yield substantial increases in disparity after Ordovician-2. This suggests that the relatively stable pattern of disparity in Fig. 1 is not likely to be an artifact of equal character weighting.

of states (Foote, 1994). That the same methodology can uncover a very different evolutionary pattern of disparity is demonstrated by analysis of blastozoan echinoderms (Foote, 1992b).

There is the potential for character choice to affect the conclusions of such a study. The characters implicitly cover many but not all aspects of functional ecology. For example, stem length, tube-foot spacing, food groove width, and branch density are considered important in determining the trophic niche of a crinoid (e.g., Lane, 1963b; Meyer, 1979; Ausich, 1980; Ausich and Bottjer, 1982, 1985; Bottjer and Ausich, 1986; Brower, 1987; Guensburg and Sprinkle, 1992; Sprinkle and Guensburg, 1992). Full stems are too seldom preserved to allow stem length to be considered consistently. However, food groove width—which is not coded because it too often cannot be determined—is inversely correlated with branching density (Ausich, 1980; Brower, 1987)—which *is* coded implicitly by a number of characters. The characters also do not explicitly include behavior (e.g., Meyer and Macurda, 1977). Nevertheless, numerous studies interpreting functional morphology on the basis of crinoid remains suggest that many important aspects of functional design are included in the character set (e.g., Lane, 1963b; Brower, 1966, 1987; Breimer, 1969; Breimer and Webster, 1975; Breimer and Lane, 1978; Meyer, 1973, 1983; Ubaghs, 1978; Ausich, 1980, 1983, 1986, 1988; Brett, 1981; Donovan, 1988, 1990; Kammer, 1985; Kammer and Ausich, 1987; Kendrick, 1992; Baumiller, 1993). Therefore, while certain aspects of ecological diversification such as tiering (Ausich and Bottjer, 1985) are not captured, many others are. It seems reasonable to conclude tentatively that any Silurian-Devonian ecological diversification (e.g., Brett, 1984) did not involve a substantial proliferation of morphological designs.

This study and its companion (Foote, 1994) add to the list of major biologic groups in which substantial disparity may have evolved early at relatively low taxonomic diversity. These include: echinoderms (Paul, 1977, 1979; Sprinkle, 1980, 1983; Campbell and Marshall, 1987; but see Smith, 1988 for another view); blastozoan echinoderms (Foote, 1992b); arthropods (Briggs et al., 1992; Wills et al., 1994; Foote and Gould, 1992); archaeogastropods (Wagner, 1993); stenolaemate bryozoans (Anstey and Pachut, 1992); and metazoans as a whole (Valentine, 1969, 1986; Valentine and Erwin, 1987). Nevertheless, this evolutionary pattern is not universal (Foote, 1993a). Assessment of the relative frequency of such early increases in disparity awaits the study of additional clades.

ACKNOWLEDGMENTS

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APPENDIX 1: Characters Used to Quantify Crinoid Form

As discussed above, 75 characters were used to describe crinoid form (Table 1). Initially, 107 characters were considered. Of these, several were found to be invariant or redundant and were omitted. In addition, I omitted several characters that were found to be difficult to code reliably, most often because they are subject to extreme preservational variability (e.g., characters concerning ornamentation) or do not seem to have been treated consistently in descriptions of species (e.g., respiratory structures, which seem less likely to be mentioned or figured in older literature). Characters such as ornament and respiratory structures are clearly important from a functional perspective, and their exclusion may seem undesirable. However, data were initially analyzed with all but the invariant characters included, and the temporal pattern of disparity was found to be essentially the same as that presented above (Fig. 1).

There is inevitable subjectivity in coding of characters, especially when discrete character states are used to divide what is best seen as a morphological continuum, and the data presented here undoubtedly differ from those which other workers would produce. However, character states were assigned using consistent criteria. In addition to the criteria discussed above, general guidelines used include the following. (1) Characters that vary within a species were generally coded according to their predominant state. (2) However, characters that seem to show a clear ontogenetic trend (such as the incorporation of progressively more fixed brachials [Brower, 1973]) were coded according to their later state. (3) The proximal part of the stem was emphasized, because the more distal portions are much less commonly preserved. For example, a stem that consists of pentameres distally but not proximally is *not* coded as pentameric.

Some more specific details about characters and character states should also be mentioned. (1) (character 2): I have not coded stems that gradually change in form along their length as xenomorphic; rather I focused on whether there is a rather sharp transition between types of columnals.

(2) (characters 42-56 and 67): Arms are considered to begin at the point where they become free and distinct from the cup. For example, in a species with no fixed brachials, and with five arms that each branch once, the number of arms is coded as 5 rather than 10. In camerates and inadunates the distinction between cup and arms is generally easy to make. However, in many species of Flexibilia it is difficult to draw a distinct boundary between the cup and the arms. In such species two criteria were used to guide judgment as to whether brachial plates should be considered part of the cup: whether they appear to be suturally united, and whether they are joined by regular interbrachial plates (not merely the polyplated perisome). (3) (character 47): The effective number of orders of branching reflects both the number of orders from a strictly geometric perspective, and the number of ultimate divisions of the arms that result. For example, consider an arm that exhibits regular bilateral heterotomy, with a main arm that gives off smaller armlets that do not themselves branch. Such an arm exhibits only one order of branching. However, suppose it produces a total of eight armlets that persist for the length of the main arm. Then, as far as the ultimate number of feeding appendages, it is as if the arm had dichotomized into two armlets, each armlet had itself dichotomized into two smaller armlets, and each of these smaller armlets had dichotomized again. In other words, it is as if the arm had three orders of branching.

Multistate characters were treated as ordered when the character states could reasonably be considered to fall along a morphological trend or gradient. For example, it is not obvious how the different states for cup symmetry (character 36) could be ordered, but it is clear that the size of the cup relative to the stem (character 38) can be ordered. Ordering of characters need not imply anything about evolutionary transitions, although it probably does in many cases. To allow equal weighting of characters in calculating phenetic distances between species, each character was scaled so that the maximal character difference between two species is equal to one unit. Therefore, ordered characters were rescaled so that their states fall between zero and one, inclusive. The number of compound radials (character 23) was first converted to a proportion of the number of radials. To emphasize proportional differences among species, characters 42, 59, and 63 were first transformed to their natural logarithms. Thus, the difference between 5 and 10 arms is considered equivalent to the difference between 10 and 20 arms but greater than the difference between 10 and 15 arms. The character difference for binary characters is equal to zero if two species have the same state, and unity if their states differ. The same is true of unordered multistate characters, with the exception of characters 6 and 7. For these two characters, character states were treated as a graded series of forms linked indirectly through circular forms. For example, according to this scheme a pentagonal stem and a pentalobate stem differ by one-half unit, a pentagonal stem and a tetralobate stem differ by one unit, circular stems differ from all other stems by one-half unit, and

elliptical stems differ from all other non-circular stems by one unit. This scheme is meant to reflect what is perceived as a set of morphological clines, not an evolutionary sequence. Because so few characters are involved, data transformations on characters like the number of arms and conventions for determining character differences, such as on the stem, have little practical effect on patterns of disparity.

In assessing morphological disparity, results depend to some extent on what is deemed a "unit" character. For example, consider characters 22 (absence or presence of compound radials) and 23 (number of compound radials [if present]). With respect to compound radials, any species lacking compound radials differs from any species possessing them by one unit [(1 + "no comparison") ÷ 1]. In contrast, species possessing different numbers of compound radials differ from each other by less than one unit, because they all have the same character state for character 22. The maximal difference between species with compound radials is then (0 + 1) ÷ 2 or 0.5. Alternatively, compound radials could have been coded with a single character. Assuming all species being compared had the same number of radials, the difference between no compound radials and one compound radial would then be the same as the difference between one and two compound radials. Thus, because the number of compound radials hinges on possession of compound radials, the manner of coding adopted here effectively attributes more weight to presence or absence of compound radials than to variations in number of compound radials. The same situation holds for other sets of characters. Several lines of evidence discussed above suggest that the large-scale temporal pattern of disparity documented in this paper is not likely to be an artifact of character choice and weighting.

APPENDIX 2: Character Data for Crinoid Species Used in this Study

Character data for crinoid species used in this study are tabulated on the following pages. Unknown states are indicated by ?; inapplicable states indicated by N. See Table 1 and Appendix 1 for explanation of characters and character states. Sources of data are listed in Appendix 3. Two-letter code preceding each species indicates higher taxonomic affinity: CL, Cladida; DB, Diplobathrida; DI, Disparida; EC, Echmatocrinida; FL, Flexibilia; HY, Hybocrinida; and MO, Monobathrida.

Genus	Species	Sources	Char.no. 1111111111222222222233333333334 1234567890123456789012345678901	4 2	4444444555555555 3456789012345678	5 9	666 012	6 3	666666777777 456789012345

Cambrian

Genus	Species	Sources	col1	c2	c3	c4	c5	c6	c7
EC Echmatocrinus	brachiatus	92	1NNNNNNNNONN1?0913?00????????????11??00001	9	00100NNN00010100	N	NNO	N	ONN10??????0

Lower Ordovician

DB Proexenocrinus	inyoensis	3,99	2?0??0?0??????15131000N2??0N501121??11101	10	00200NNN00110101	4	111	1	ONN3????????
CL Aethocrinus	moorei	76,106,107	20101760?0NN0N15111000N2500N501112?500011	5	00201?0N00010101	2	110	N	ONN?01100110
CL Compagicrinus	fenestratus	45	2?001??0?0NN??15111101112?112501311?500011	5	0010110N00020100	N	NNO	N	ONN201?1????
DI Ramseyocrinus	cambriensis	28,29	2010154000NN0N150N0000N141NNNNN001?500001	5	0000120N00020100	N	NNO	N	ONN30???????

Ordovician-2

DB Anthracocrinus	primitivus	60	2?1000?010NN??15131010N2500N501220?511101	15	00100NNN00110101	12	111	1	ONN20100??10
DB Archaeocrinus	subovalis	60	2?1000?010NN??151310?0N25?0N5?11210511101	10	0020120N00100101	10	111	1	ONN20???????
DB Bromidocrinus	nodosus	60	2010067010NN??15131000N1500N5013310611101	10	0???0NNN1NN?0101	7	111	?	ONN?010?0010
DB Cleiocrinus	bromidensis	60	2?????7701?????15131000N?5013501?11?511101	?	0????????????????1	12	ON?	?	ONN?0???????
DB Diabolocrinus	arbucklensis	60	2?1?007010NN??15131000N2500N501120051111	10	00100NN1NN00101	3	111	1	0NN301000110
DB Gustabilicrinus	plektanikaulos	42	2010006010NN??15131000N1500N501121?611001	20	00200NNN00100101	10	111	1	ONN10?????1?
DB Pararchaeocrinus	decoratus	60	2?10000010NN??15131000N25?0N5013200501101	10	0020120N1NN00101	6	111	1	0NN30100?010
DB Reteocrinus	variabilicaulis	42	2010107000NN1215131000N15013501111?501111	20	0010120N00020101	8	100	N	ONN10?????11
MO Abludoglyptocrinus	gregatus	42	201000?010NN??150N0000N250NNNNN021?501101	10	00200NNN00100101	8	111	?	ONN?0?????1?
MO Colpodecrinus	quadrifidus	97	2010155010NN??150N1000N2400N401011160101	10	00201?1100000101	6	110	N	ONN?0???????
FL Archaeotaxocrinus	burfordi	65	2010100010NN??15111011115011501211?500001	5	00001?0N00000101	2	110	N	ONN?010?????
CL Carabocrinus	treadwelli	96	2010007010NN??15111000N25111501331150101	5	0020121000000100	N	NNO	N	ONN100NNNN00
CL Cupulocrinus	jewetti	25	20100070?0NN??15111101112500N501211?501011	5	0010120N00000100	N	NNO	N	ONN3010110??
CL Eopinnacrinus	pinnulatus	26	2?1000?010NN??15111100112500N501210?501001	5	0010100N00100100	N	NN1	1	ONN3010??01?
CL Palaeocrinus	hudsoni	96	2?10007010NN??15111000N2500N5012310501011	5	0110120N00000100	N	NNO	N	ONN100NNNN00
CL Porocrinus	bromidensis	96	2100000010NN??15111000N2500N5012310501011	5	00200NNN00010100	N	NNO	N	ONN200NNNN00
CL Quinquecaudax	glabellus	26	2010177010NN111511101112500N501111?500001	5	0010120N00010100	N	100	N	ONN3010110??
DI Acolocrinus	crinerensis	94	2?0?0000??????150N01015231NNNNN1321611001	45	20000NNN00020100	N	NNO	N	ONN01NNNN00
DI Agostocrinus	xenus	50	2?0??000??????15110000N230NNNNN1210511001	75	20000NNN00020110	N	NNO	N	ONN?0?????00
DI Apodasmocrinus	daubei	112	2?10167010NN??150N00013250NNNNN1312511001	5	0000100N00000101	1	ON1	1	ONN3010110??
DI Calceocrinus	longifrons	23	200000?0?0NN??140N0011224?NNNNN002?100001	3	01001?1000020100	N	NNO	N	ONN?010??0??
DI Columbicrinus	crassus	42	20100070?0NN12150N0012150NNNNN1210500001	5	0000100N00110100	N	NN1	1	0NN3010000??
DI Cremacrinus	arctus	58	200000?0?0NN??150N0011324?NNNNN0011101001	4	0200111000000100	N	NNO	N	ONN3010110??
DI Doliocrinus	pustulatus	112	2?10166010NN??150N0012150NNNNN1210500001	5	0?10???0002?100	N	NN?	?	ONN?010??010
DI Ibexocrinus	lepton	62	2?001??0?0NN??150N00013250NNNNN101?500001	5	0000121000000100	N	NNO	N	ONN300NNNN??
DI Iocrinus	shelvensis	79	2010067?0?0NN??150N00111250NNNNN011?500001	5	0010120N00000100	N	NNO	N	ONN30101?0??
DI Paracremacrinus	laticardinalis	23	200000?0?0NN11150N0011124?NNNNN0001101001	4	0100111000110100	N	NNO	N	ONN3010??0??
DI Peltacrinus	sculptatus	112	20101000?0NN??150N0011N250NNNNN020?601001	5	0010120N00000100	N	NNO	N	ONN3010?00??
DI Penicillicrinus	parvus	112	201000?0?0NN??150N00013150NNNNN111?501001	5	0000120N00020101	1	ON0	N	ONN301??????
DI Praecursoricrinus	sulphurensis	112,36	20100670?0NN??150N0012150NNNNN111?500001	5	0010100N00110100	N	NN1	1	ONN3010?????
DI Tryssocrinus	endotomitus	42	2010007000NN12150N0012150NNNNN111?500001	5	0010121100010101	1	ON0	N	ONN3010100??
HY Hybocrinus	nitidus	95	2000007010NN12150N0001251NNNNN1310501001	5	00200NNN00020100	N	NNO	N	ONN100NNNN00
HY Cornucrinus	mirus	75,80	20000070?0NN??150N00111241NNNNN0312001000	N	NNNNNNNNNNNNNNNN	N	NNN	N	130N1NNNNN00

Ordovician-3

	Genus	species	n							
DB	Archaeocrinus	microbasalis	110	2010007020NN??1513000N2500N5011?1?511111	10	0020110N1NN00101	10	111	1	0NN10???????
DB	Cleiocrinus	regius	85	2100060?0NN1351513000N0501350111?0501101	40	00100NNN00100101	25	0N1	1	0NN20???????
DB	Gaurocrinus	nealli	110	2100620?0NN??1513000N2500N5011?1?50501101	10	00100NNN00100101	10	101	1	0NN200NNNN10
DB	Ptychocrinus	fimbriatus	21	2010007010NN??1511000N2500N50111?2501101	10	00200NNN00110101	4	111	1	0NN20???????
DB	Simplococrinus	persculptus	46	2110067000NN??1513000N1500N5011?10501111	20	00100NNN1NN00101	12	111	1	0NN200NNNN10
MO	Alisocrinus	tetrarmatus	21	2110007010NN??2150N0000N24?NNNN111?501101	20	00100NNN00110101	8	111	1	0NN20???????
MO	Canistrocrinus	typus	110	2110007010NN??2150N0000N247NNNN121?501101	20	00100NNN00100101	10	101	1	0NN10?????0?
MO	Eopatelliocrinus	scyphogracilis	21	2100006010NN??2150N0000N231NNNN011?501011	20	00100NNN00100101	5	111	1	0NN20???????1?
MO	Macrostylocrinus	pristinus	21	2100007010NN??2150N0000N231NNNN011?501101	10	00100NNN1NN00101	5	111	1	0NN20???????
MO	Macrostylocrinus	wyomingensis	59	2920202012????NN??2150N0000N250NNNN0201511001	10	00100NNN1NN00101	4	111	1	0NN30???????
MO	Periglyptocrinus	billingsi	110	2920202020NN??2150N0000N250NNNN0?12501111	20	00200NNN1NN00101	7	111	1	0NN20???????
MO	Pycnocrinus	dyeri	88,110	2010007070NN??2150N0000N250NNNN021?501101	10	00200NNN00100101	10	111	1	0NN200NNNN10
MO	Xenocrinus	penicillus	110	2920570?2????2150N0000N24?NNNN111?501101	10	00200NNN00100101	12	101	1	0NN100NNN10
FL	Protaxocrinus	laevis	89	2920000010NN??2150N0000N250NNNN001?101001	10	00100120N00100101	2	100	N	0NN201000010?
CL	Cupulocrinus	crossmani	24	2100006010NN1251511011123?0N5112?1?501001	5	00100120N00000101	N	NN0	N	0NN301010010
CL	Dendrocrinus	rugocyathus	79	2110072020NN??151511011112500N50121?501011	5	00201200N0020100	N	NN0	N	0NN301?11?0??
CL	Grenprisia	billingsi	25,86	2110166010NN??151511011112500N50131?500001	5	00101210000000100	N	NN0	N	0NN30111?0??
CL	Illemocrinus	amphiatus	31	2100062020NN12151511000N2500N50122115010011	5	00201200N0010100	N	NN0	N	0NN701011000
CL	Porocrinus	conicus	49	2100062020NN12151511000N2500N50121?1501001	5	00201200N0010100	N	NN0	N	0NN0?010110 00
CL	Praecupulocrinus	conjugans	24	2100006010NN12151511011112500N50131?0?500001	5	00101200N0020100	N	NN0	N	0NN301010010?
DI	Calceocrinus	multibifurcatus	20	2000002070NN??2140N0011224?NNNN001?101001	3	0200121000010100	N	NN0	N	0NN301070?0??
DI	Cincinnaticrinus	varibrachialus	113	2010102020NN12150N00012250NNNN1111500001	5	0000121000020100	N	NN0	N	0NN201000000
DI	Cremacrinus	punctatus	25	2010102020NN??2150N00011324?1NNNN001?101001	4	0200121000010100	N	NN0	N	0NN301070?0??
DI	Daedalocrinus	bellevillensis	113	2010166070NN??2150N0000132?50NNNN1107500001	5	0010121100010100	N	NN0	N	0NN301?11?00?
DI	Dystactocrinus	constrictus	113	2101072070NN??2150N0001225?0NNNN1117500001	5	0000121000110101	1	0N0	N	0NN301010010?
DI	Ectenocrinus	simplex	113	2101072070NN??2150N0000132?50NNNN1117500001	5	0000100N00110101	1	0N1	1	0NN301?10?0??
DI	Isotomocrinus	tenuis	113	2010166020NN??2150N0000132?50NNNN1117500001	5	0010120N00020100	N	NN0	N	0NN301010?0??
DI	Ohiocrinus	laxus	113	2010007070NN??2150N0001225?0NNNN1117500001	5	0000111000010101	2	0N0	N	0NN301110?0??
DI	Sygcaulocrinus	typus	113	2100002170NN??2150N0001315?0NNNN101?500001	5	0?00111000020100	N	NN0	N	0NN30????????
HY	Hybocystites	eldonensis	86	2000002070NN??2150N00011250NNNN1311501001	3	00200NNN00020100	N	NN0	N	141000NNN00

Llandoverian

	Genus	species	n							
DB	Nexocrinus	delicatulus	30	2010000010NN??151511000N2570N5111?1?2501101	20	00100NNN00010101	6	111	1	0NN20???????
DB	Ptychocrinus	medinensis	17	2100070200NN0N15151511000N2500N5011?121?501111	20	00200NNN00100101	8	111	1	0NN200NNNN10
DB	Silfonocrinus	siluricus	4	2010072020NN??151513000N2500N5011?1?50501101	20	00100NNN00100101	2	101	?	0NN30???????
DB	Stereoaster	squamosus	4	2???200????????2150N0000N231NNNN0201611001	20	0???1?0N1NN00101	8	11?	?	0NN20???????
MO	Clematocrinus	ohioensis	6	2010007110NN??2150N0000N231NNNN021051?1101	10	00100NNN1NN10101	2	111	1	0NN200NNNN1?
MO	Kylixocrinus	latus	30	2100070110NN??2150N0000N231NNNN020511001	10	00200NNN1NN10101	4	111	?	0NN30???????
MO	Manticrinus	exaitos	6	2700002070NN??2150N000150NNNN141NNNN012?601101	10	00?00NNN1NN00101	7	111	?	0NN200NNNN10
MO	Stipatocrinus	hulveri	34	2000002070NN??151511011123?0N5011?121?501001	10	00200NNN00110101	9	101	1	0NN201000110
FL	Clidochirus	springeri	2	2210070100NN??151511011123?0N5012?1?501001	5	0010120N00000101	1	0N0	N	0NN201000010
FL	Protaxocrinus	cataractensis	30	2010002020NN??151511011112500N50111?2501001	5	0010120N00010100	N	NN0	N	0NN201020010?
CL	Dendrocrinus	parvus	30	2010000020NN??2151111000N2500N50131?501001	5	0010120N00020100	N	NN0	N	0NN301?11?0??
CL	Euspirocrinus	heliktos	5	2010000020NN??151511110?10N1500N5Q1211?600001	5	0010120N00010100	N	NN0	N	0NN20?1?100??
CL	Kanabinocrinus	thyaros	5	2100000020NN??2150N000011101100	5	0010120N00000100	N	NN0	N	0NN20?1?11???
DI	Calceocrinus	incertus	1	2700002070NN??2140N0011224?1NNNN0011101001	3	0200121000010100	N	NN0	N	0NN20?10?0?0??

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DI Cataractocrinus    clementi          30         2010007010NN11150N000152??NNNNN001?600001   4 00001?0N00020100   N NNO   N ONN3010100??
DI Diaphorocrinus     pleniramulus      30         201000?0?0NN??140N00112231NNNNN001?101001   3 0200121000010100   N NNO   N ONN3010??0??
DI Eomyelodactylus    murrayi           32         21011060?0NN??150N00011150NNNNN111?500001   5 0000120N00010101   1 ONO   N ONN301?100??
DI Pariocrinus        heterodactylus    30         20100000?0NN??150N00111150NNNNN111?500001   5 00001?1?000010100  N NNO   N ONN3010100??
DI Trypherocrinus     brassfieldensis   1          20000000?0NN??150N00113231NNNNN101?101001   3 0200121300020100   N NNO   N ONN301??????

Wenlockian
DB Lyriocrinus        melissa           110        2?0000?0?0NN??15131000N2500N5011200611001  10 00000NNN1NN00101   4 111   1 ONN10????10
MO Barrandeocrinus    sceptrum          103        2000006010NN??15110000N131NNNNN0110501001  10 00110NNN1NN01301   4 111   1 ONN200NNNN10
MO Closterocrinus     elongatus         69         201000?0?0NN??150N0000N141NNNNN012?500001  10 00100NNN1NN00101   6 110   N ONN10???????
MO Marsupiocrinus     coelatus          90         20100070?0NN??150N0000N21NNNNN0200611001  20 10100NNN1NN00101   8 111   1 ONN200NNNN10
MO Patelliocrinus     ornatus           90         2????0?0?0?????150N0000N231NNNNN0100601001  10 00100NNN1NN00101   4 111   1 ONN20???????
MO Periechocrinus     costatus          75         2?1000?010NN??15110000N230NNNNN111?501101  40 00100NNN1NN00101   8 110   N ONN?011?0110
MO Polypeltes         granulatus        104        2?00000010NN??150N0000NNNNNNNNN0200601001  20 0000100N1NN00101  17 111   1 ONN?0???????
MO Promelocrinus      anglicus          22         20100070?0NN??150N0000N241NNNNN011?601101  20 021012121NN00101  10 111   1 ONN20???????
FL Anisocrinus        interradiatus     89         2????0???????15111001123110N501131050100120 00100NNN0N00000101   6 110   N ONN00??????0
FL Asaphocrinus       ornatus           89,75      201000?0?0NN1115111000N2310N501221?501001   5 0010120N00000100   N NNO   N ONN201??????
FL Calpiocrinus       intermedius       89         2010007010NN13150N1000N2310N5000200601001  10 0000121100000101   4 110   N ONN10???????
FL Cholocrinus        obesus            89         201000?010NN1315111000N2310N500111?501001   5 0210121000000100   N NNO   N ONN200NNNN11
FL Clidochirus        pyrum             89         201000?0?0NN??15111011123110N5011110501001 20 0000100N00000101   6 ONO   N ONN10???????
FL Homalocrinus       parabasalis       89         2010007010NN??151110111231125001210501001  10 0000111100000101   3 110   N ONN10???????
FL Icthyocrinus       laevis            89         2000005010NN??150N1000N2310N500020160110140 0000100N01000101  13 ONO   N ONN20???????
FL Lecanocrinus       macropetalus      89,75      20100000?0NN??15111000N2310N5012200501001   5 0000120N00000100   N NNO   N ONN10???????
FL Lithocrinus        divaricatus       89         2?1000?0?0NN??15111000N2310N5001111501001  10 0010121400000101   4 110   N ONN10?????1?
FL Meristocrinus      interbrachiatus   89         2?0000?0?0NN??15111011123110N501211?500001   5 0010120N00000101   1 100   N ONN20?????1?
FL Mysticocrinus      wilsoni           90         2????00??????15111101123110N5001311501001   5 0110100N00010100   N NNO   N ONNO00NNNN?0
FL Protaxocrinus      salteri           89         201000?0?0NN??151210011231100N5102112501001 10 0010120N00000101   3 100   N ONN2010?????1?
FL Pycnosaccus        bucephalus        89         201000?0?0NN??151110000N2310N500210?501011   5 0010120N00000100   N NNO   N ONN10?????1?
FL Sagenocrinites     expansus          89         2?100060?0NN??15111000N23115002110501001  20 0010120N00000101   8 110   N ONN20?????1?
FL Temnocrinus        tuberculatus      89         200000?0?0NN??151110111231100N5011100501001 10 0010120N00000101   2 110   N ONN10?????10
CL Botryocrinus       ramosissimus      12         2010006010NN??15111000N2500N5002112501001   5 0010121000010100   N NNO   N ONN301011010
CL Cyathocrinites     acinotubus        11         2?10007010NN??15111000N2500N5011212501001   5 0020120N00010100   N NNO   N ONN3010100??
CL Dictenocrinus      decadactylus      9          2010066010NN1115111000N2500N501211?500001   5 0010100N00110100   N NN1   1 ONN301111022
CL Enallocrinus       scriptus          109        2?0?0000??????15111000N1500N5021100500001   5 1000120N00000100   N NNO   N ONN30?????10
CL Eoparisocrinus     siluricus         5,90       2?100070?0NN??15111000N2500N501311?501001   5 0010120N00020100   N NNO   N ONN2010100??
CL Euspirocrinus      spiralis          12         201000?010NN1215111000N2500N5003111500001   5 0010120N00000100   N NNO   N ONN201010000
CL Gissocrinus        luculentus        78         200000?0?0NN1115111000N2310N501121?501001   5 0010120N00010100   N NNO   N ONN3010110??
CL Mastigocrinus      loreus            10         201010?010NN??15111000N1500N5011111?500001   5 0010120N00000101   N NNO   N ONN3011101?
CL Petalocrinus       mirabilis         13         2???06601?????150N1000N2??0N5000202611001   5 0010120NNNNN1100   N NNO   N ONN200NNNNO0
CL Thalamocrinus      robustus          71         201006?0?0NN??15111000N0500N5022310500001   5 0010120N00010100   N NNO   N ONN2010010??
CL Thenariocrinus     callipygus        7,8        2010100010NN1115111000N25011501211?500001   5 0010120N00000100   N NNO   N ONN301111101?
DI Calceocrinus       chrysalis         19         200000?010NN12140N00112240NNNNN001?101001   3 0200121000010100   N NNO   N ONN2010?00??
DI Charactocrinus     pustulosus        19         2?000000?0NN??140N00112230NNNNN001?110100   3 0200120N00020100   N NNO   N ONN3010100??
DI Crinobrachiatus    brachiatus        33         210100?0?0NN12150N0000N250NNNNN111?500001   5 0010120N00020100   N NNO   N ONN301011????
DI Eohalysiocrinus?   typus             19         2?0000?010NN??140N00111231NNNNN001?101001   3 0200121000020100   N NNO   N ONN?010??0??
DI Herpetocrinus      fletcheri         12,74,91   211110?010NN??140N00111240NNNNN0?1?100001   4 0100121?00010100   N NNO   N ONN30101?0??
DI Homocrinus         parvus            113        200000?0?0NN??150N00013150NNNNN112?500001   5 00100NNN00030101   1 ONO   N ONN30???????
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Class	Genus	Species	Ref	String 1	N	String 2	N	Code	N	String 3
DI	Paracolocrinus	paradoxicus	18	2????000?????150N01015231NNNN1310611001	20	20000NNN00020100	N	NNO	N	0NN01NNNN?0
DI	Pisocrinus	pillula	90	2000000070NN??150N0111125?1NNNNN0310611001	5	00000NNN00030100	N	NNO	N	0NN301010000

Upper Silurian

Class	Genus	Species	Ref	String 1	N	String 2	N	Code	N	String 3
DB	Dimerocrinites	planus	90	2000007070NN??2715111000N2500N50112125011011	10	00100NNN1NN00101	6	111	1	0NN200NNNN?0
DB	Eudimerocrinus	multibrachiatus	75,90	2070062070NN??2715111000N2500N50111125111011	10	0010120N1NN00101	5	111	1	0NN300NNNN?0
DB	Gazacrinus	ramifer	90	2070062070?????2715111000N2500N50112125?0111	10	00000NNN1NN00101	4	110	N	0NN200NNNN01
DB	Lampterocrinus	tennesseensis	90	2070062070?????2715111000N2500N5011212?501111	5	0020121000000201	2	111	2	0NN301110110
DB	Nyctocrinus	magnitubus	90	2?1?000070NN??2715N1000N2500N50101161100?	10	1010110N1NN00100	N	NN1	1	0NN301110??
MO	Allocrinus	longidactylus	90	2000000070NN??2715N1000N0000N231NNNNN020161100?	10	00100NNN00010101	4	111	6	0NN30???????
DB	Bohemicocrinus	pulverens	75,108	2010000010NN??2715110000N230NNNNN1210501001	10	0020120N00000101	10	111	2	0NN1107?????
MO	Carpocrinus	petilus	35	2010007070NN??2715110000N0000N237NNNNN1207501001	10	00100NNN00000101	4	111	2	0NN200NNNN??
MO	Ctenocrinus	gottlandicus	105	2010007010NN??2715110000N0000N237NNNNN011?601111	10	00201121NN00101	5	111	1	0NN30?????10
MO	Desmidocrinus	pentadactylus	35	2000007010NN??2715110000N0000N247NNNNN1212?511001	40	00000NNN00100101	10	110	1	0NN110?????
MO	Eucalyptocrinites	ventricosus	90	2??????2?????????150N0000N241NNNNN0201601001	20	00200NNN1NN00101	2	0N1	2	0NN200NNNN01
MO	Lyonicrinus	bacca	90	2010000070NN1150N0000N231NNNNN0201601001	10	10100NNN1NN00201	2	111	1	0NN300NNNN10
MO	Marsupiocrinus	stellatus	90	2010007070NN??2715111000N2310N5003107501001	5	0010120N01000100	N	NNO	N	0NN201010012
FL	Asaphocrinus	bassleri	89	2010007070NN1115111000N2310N50112005010011	5	0010120N00010100	2	110	N	0NN301010??
FL	Gnorimocrinus	cirrifer	89	2010007070NN??2715110011231N500111?501001	10	0010110N00000101	N	NNO	N	0NN20102??21?
FL	Hormocrinus	tennesseensis	89	2?10007010NN??2715111000N230N5012101501011	5	0010120N00000100	1	100	N	0NN201010?00??
FL	Protaxocrinus	robustus	89	2010007010NN??2715111000N1500N5012111750001	5	0010120N00000100	N	NNO	N	0NN10?????1?
FL	Pycnosaccus	patei	89	2010007070NN??2715111000N2500N5012111750001	5	0010120N00020100	N	NNO	N	0NN301010002
CL	Anthomocrinus	tenuis	12	2?10007070NN??2715110011250N5011112500001	5	0010100N00010100	N	NN1	N	0NN301?100??
CL	Gothocrinus	gracilis	12	2000007070NN??2715110011324?NNNNN0017101001	4	0200121000110100	N	NNO	N	0NN201010002
DI	Cremacrinus	tubuliferus	90	2000007070NN??140N0011223?NNNNN0017101001	3	0200120N00020100	N	NNO	N	0NN201010?0??
DI	Grypocrinus	multibrachiatus	20	2000007070NN??150N0111125?0NNNNN0311511001	N	00000NNN00030100	N	NNO	N	0NN10?????700
DI	Pisocrinus	quinquelobus	90	2000007070NN??140N0011223?1NNNNN0017101001	3	0200121000020100	N	NNO	N	0NN301010??
DI	Synchirocrinus	foerstei	73,90	2000007070NN??140N0011223?1NNNNN0017101001						

Lower Devonian

Class	Genus	Species	Ref	String 1	N	String 2	N	Code	N	String 3
DB	Ambicocrinus	arborescens	37	201006?0?0NN??1511000N2500N5011?1?500101	10	0020110N1NN00101	6	111	1	0NN20???????
DB	Bogotacrinus	scheibei	68	2?120070?1????2715111000N2500N2??0N501120751101	10	0020121000000101	5	111	2	0NN20???????
DB	Macarocrinus	terfurcatus	82	2?1??0?070NN??2715111000N2500N5011201251501001	10	0020110N00010101	2	111	1	0NN30???????
DB	Orthocrinus	tuberculatus	83	2?1??0?070NN??2715111000N2500N5021121750501	10	00100NNN00010101	6	111	2	0NN20???????
DB	Rhodocrinites	nortoni	38	2??????0?0?????2715131000N11N13501020061111	10	0010110N1NN00101	20	111	?	0NN70???????
DB	Spyridiocrinus	oehlerti	101	2000007010NN??2715131000N2500N5011300061001	40	00000NNN1NN00101	11	111	1	0NN?0???????
DB	Thylacocrinus	vannioti	63	2?10207010NN??2715131000N2500N501131050501001	24	00100NNN1NN00100	N	NN1	1	0NN301100110
MO	Cordylocrinus?	plumosus	37	2010207011??2?150N0000N231NNNNN0200501001	10	0020100N00010100	5	111	2	0NN201072110
MO	Ctenocrinus	arduennensis	27	2?10007010NN??2715150N0000N24?NNNNN0111501111	15	0210210N1NN00101	4	111	1	0NN200NNNN00
MO	Culicocrinus	nodosus	83	2000007010NN??2715110000N230NNNNN031?611001	10	0010110N1NN00101	18	111	1	0NN20???????
MO	Gennaeocrinus?	germanicus	83	2?10202070NN??1150N0000N231NNNNN0??17601001	20	00100NNN1NN00101	N	NN1	1	0NN30???????
MO	Hapalocrinus	frechi	44,82	2000007070NN1150N0000N231NNNNN0??17600101	10	0020110N00020200	5	111	1	0NN100NNNN10
MO	Macrostylocrinus	recumbens	91	2?100?0?0?????2715N0000N231NNNNN011?501111	25	00000NNN1NN20301	10	111	1	0NN20???????
MO	Melocrinites	nobilissimus	37,110	2?1??0?010NN??2715N0000N240NNNNN011?501111	15	02201212NN00101	2	111	1	0NN20???????
MO	Oenochoacrinus	princeps	16	2??????0?0?????2715110000N2500N50112121NN00201	10	001012??1NN00201	6	111	1	0NN70???????
MO	Pithocrinus	ovatus	16	2?1?207010NN??2715N0000N231NNNNN021?501001	20	00101214?1NN00101	22	111	1	0NN701170110
MO	Scyphocrinites	elegans	88	200000601?0NN12150N0000N24?NNNNN022?601111	10	0020120N00000101				0NN30???????

	Genus	Species	Ref	Code string							Trailing code
MO	Tryblocrinus	flatheanus	16	2010000?0NN111150N0000N?31NNNN020061100	10	001012101NN00201	25	111	1	ONN?00NNNN10
FL	Clidochirus	schucherti	89	201002?0?0NN??1511101112329N5011110501001	35	0000170N00000101	12	ONO	N	ONN107??????
FL	Miracrinus	perdewi	14	2????0?01???????15111000N2??0N50122005011001	10	000011ON00000101	2	ONO	N	ONN20??????
FL	Pycnosaccus	tenuibrachiatus	89	2????02?0?0NN??715111000N1500N50211?2501001	5	0020120N00030100	N	NNO	N	ONN30171107?
CL	Bactrocrinites	jaekeli	44,82	2000?0?0?0NN??715111000N1500N2500N50121??501011	5	00101?7?00010100	N	NNO	N	ONN30101101?
CL	Botryocrinus	schultzei	43	201026?0?0NN??715111000N2500N501311?501001	5	0010100N00020100	1	NN1	1	ONN30171107?
CL	Bridgerocrinus	sp	111	2????02?0?0NN??715111000N2500N50131?7501001	5	0020120N00010100	N	NNO	N	ONN20??????
CL	Codiacrinus	schultzei	82	2000002?010NN??7150N1000N2310N50101?7601001	5	00201?0N00010100	N	NNO	N	ONN30171107?
CL	Dictenocrinus	hystrix	82	201026?020NNON151110000N2500N50121115011001	5	00101110000010100	N	NNO	N	ONN301010000
CL	Eifelocrinus	dohmi	43	201026?020NNON??715111000N2500N50121115011001	5	0010110000010100	N	NNO	N	ONN30171107?
CL	Follicrinus	kayseri	44,82	201002?0?0NN??715111000N1500N2310N50111?7501001	5	00101?0N00020100	N	NNO	N	ONN30171107?
CL	Gissocrinus	vertebrachialis	82	201002?0010NN??715111000N2500N50122117501001	5	0010120N00020100	N	NNO	N	ONN30??????
CL	Idaeumocrinus	rotundus	64	2??062?0?0?0NN??715111000N2500N5011117501001	5	0010100N00010100	N	NN1	?	ONN30??????
CL	Imitatocrinus	gracilior	82	201002?0?0NN??715111000N2??0N50111?7501001	5	0010100H00010100	N	NN1	1	ONN30171107?
CL	Lasiocrinus	scoparius	37	2010000?020NN??715111000N1500N50121115011001	5	0010121000010100	N	NNO	N	ONN30101007?
CL	Nassoviocrinus	pachydactylus	43	2?10026?020NN??715111000N2500N50121117501001	5	00101?7?00020100	N	NNO	N	ONN?01??2007?
CL	Pagecrinus	gracilis	55	201026?020?0NN??715111000N1500N50211?7500001	5	0000121000010100	N	NNO	N	ONN20101007?
CL	Parisangulocrinus	zeaeformis	82	2??00?0?0?0NN11151110000N50131?7500001	5	1020120N00010100	N	NNO	N	ONN30101107?
CL	Propoteriocrinus	follmanni	83	2?1?26?020?0NN??715111000N2500N50232117501011	5	0010121000010100	N	NN1	1	ONN30101107?
CL	Rhadinocrinus	nanus	82	202002?020?0NN??715111000N2500N50131?7501001	5	0010121000020100	N	NNO	N	ONN30101007?
CL	Rhenocrinus	ramosissimus	43	202002?020NN??715111000N1500N50231?7500001	5	0010121000000100	N	NNO	N	ONN30101107?
DI	Calycanthocrinus	decadactylus	82	2000?0?0?0NN??7190N0011231NNNN011?501001	9	00000NNN00030100	N	NNO	N	ONN30??????
DI	Espanocrinus	lemonei	116	2??000?0?0NN??140N00112230NNNNN001110100 1	3	0200101300000100	N	NNO	N	ONN301000007?
DI	Myelodactylus	keyserensis	91	2?1?70?020?0NN??715N00111250NNNNN020?100001	5	020012100000100	N	NNO	N	ONN30101107?
DI	Senariocrinus	maucheri	73,82	2000?0?020NN0N140N00112210NNNNN001?101001	3	021010N00030100	N	NN1	1	ONN301010007?
DI	Triacrinus	elongatus	82	201002?0?0NN??715150N00111230NNNNN01?501001	5	0000NNN00030100	N	NNO	N	ONN30??????

	Genus	Species	Ref	Code string							Trailing code
DB	Gilbertsocrinus	ohioensis	53	2?10002?020NN??715131000N2??0N50110511111	10	0020100N1NN10101	4	111	1	ONN20?????10
DB	Griphocrinus	nodulosus	37,56	2????07?????????7151310000N2500N50111105011101	10	0020120N1NN00101	8	110	1	ONN20?????7?
DB	Opsiocrinus	mariana	53,54	2?1?06001ON??715131000N2500N50111105011001	10	00100NN1NN00101	4	111	1	ONN30?????71?
DB	Rhipidocrinus	crenatus	15,84	2020070172???715131000N2IN13500121060011001	20	021012100000101	13	111	1	ONN20ONNNN10
MO	Aorocrinus	formosus	37	2????02?0?0NN??715110000N230NNNNN111105011101	10	00100NN1NN00101	6	111	1	ONN300NNNN10
MO	Arthroacantha	carpenteri	53,98,110	201002?020NN??715150N0000N231NNNNN02105011001	10	0020110N1NN00101	3	111	1	ONN300NNNN10
MO	Boliviacrinus	isaacsoni	70	2010002?0111?27150N0000N21NNNNN021160011001	20	00100NN00100101	5	111	1	ONN301110101?
MO	Clarkeocrinus	troosti	37	2????02?????????715110000N230NNNNN121105011101	20	00200NN1NN00101	4	111	2	ONN20?????71?
MO	Corocrinus	nodosus	53	2?12002?0?????715110000N230NNNNN1210501101	20	00200NN1NN00101	4	111	1	ONN20?????717
MO	Cyttarocrinus	jewetti	37,39,57,75	2????02?12???715110000N230NNNNN021160011001	5	0010100N00100101	1	111	1	ONN?00NNNN10
MO	Dolatocrinus	triangulatus	47,48,110	2?1?00701ON??715150N0000N240NNNNN020061011001	15	00100NN1NN00101	3	111	1	ONN?00NNNN10
MO	Eucalyptocrinites	rosaceus	84	2010007010N??1151110000N230NNNNN111?50111	20	00000NN1NN00101	5	111	1	ONN200NNNN01
MO	Gennaeocrinus	eucharis	37	2000?02010N??715110000N230NNNNN121150011001	40	07101110000100	2	111	?	ONN200NNNN10
MO	Hexacrinites	limbatus	84	2????07?1?????715110000N230NNNNN120050011001	16	00101?0N1NN00101	6	111	1	ONN301100101?
MO	Megistocrinus	depressus	37	2010?00020NN??715110000N230NNNNN111150101	10	00101211NN00101	4	111	1	ONN201100210?
MO	Thamnocrinus	springeri	37,41	2011010100NON151111112200N300230110001	5	0200110N000000100	N	NNO	N	ONN001000020?
FL	Ammonicrinus	wanneri	102	2???07??????715121000N2??0N5100201511001	10	000011110000101	1	110	N	ONN30?????71?
FL	Dactylocrinus	excavatus	89	2000006010N??7151210000N2310N510011050011001	35	000017?0N01000101	11	110	N	ONN10??????

	Genus	species	refs	data
FL	Eutaxocrinus	whiteavesi	89	2000000?0?0NN??215121000N2310N5110102500001 5 0010120N01000100 N NN0 N 0NN3010?20??
FL	Geroldicrinus	roemeri	89	20?0000?01??2?NN??215111000N2310N5002101501001 5 0000110N00000100 N 0N0 N 0NN110??????
FL	Synaptocrinus	nuntius	89	2000000?0?0NN??215121000N2310N5100210611101 40 0000100N00000101 N 110 11 0NN007??????
FL	Taxocrinus	lobatus	37,89	2000000?0?0NN??215121000N2310N5100?1?501001 5 0010120N01010101 N 110 2 0NN301010?0??
CL	Ancyrocrinus	bulbosus	72	2010045010NN12151110 00N1410N5012110500001 5 0010120N00020100 N NN0 N 0NN301011 0??
CL	Arachnocrinus	bulbosus	37,87	2010005?0?0NN??2150N1000N21N0N5010310600 1001 5 0000120N00000100 N NN0 N 0NN31NNNNN??
CL	Botryocrinus	nycteus	37	2010000?010NN??215111000N2500N50121?1?501001 5 0020121000020100 N NN0 N 0NN?01011 0??
CL	Costalocrinus	sentosus	67	22121?7?010NN??215111000N2500N5112220?501011 5 0020121000020100 N NN1 N 0NN30101107?
CL	Cupressocrinites	crassus	84	2010045010NN??215111000N50000N21N0N500002161 1001 5 0010100N00020100 N NN1 8 0NN30??????00
CL	Decadocrinus	oaktrovensis	114	2010006?0?0NN??215111000N2500N5012111?500001 5 0010120N00010100 N NN1 1 0NN301011 0??
CL	Lecythocrinus	briareus	84	2?0004501 0NN??215111000N2?70N500320?500001 5 0010120N00010100 N NN0 N 0NN301010 0??
CL	Logocrinus	geniculatus	37	2010000?010NN??215111000N2500N50121?1?501001 5 0020100N00120100 N NN0 N 0NN301?20??
CL	Nuxocrinus	crassus	66	2010000?010NN??215111000N2500N5012111?501001 5 0110120N00020100 N NN0 N 0NN301011 000
CL	Proctothylacocrinus	longus	53	2?1000600?0NN??215111000N2500N5013111?501001 5 0020120N00000100 N NN1 1 0NN301011 0??
CL	Pyrenocrinus	bethaniensis	66	2010020?010NN??215121000N21N0N5111212?501001 5 0010100N00010100 N NN0 N 0NN301010 0??
CL	Quantoxocrinus	ussheri	115	2010005?0?0NN??2150N1000N21N0N5010300601001 5 00100NNN00020100 N NN1 1 0NN301010??
CL	Rhopalocrinus	gracilis	84,89	2???0?0??????N??2?140N0011123 1NNNNN001?101001 3 00000NNN00020100 N NN0 N 0NN?01110 1??
CL	Schultzicrinus	typus	37,87	2000000?0?0NN??2140N0011?231NNNNN001?101001 3 02001210000 10100 N NN0 N 0NN?011 10??
DI	Cunctocrinus	fortunatus	51	2000000?0?0NN??2140N0012231NNNNN001?101001 3 02001210000 20100 N NN0 N 0NN?010?20??
DI	Deltacrinus	clarus	37,73	2?20?0?0??????N??2?140N0011?230NNNNN001?101001 3 02001210000 20100 N NN1 N 0NN30???????
DI	Deltacrinus	secundus	37,73	2?2000?0?0NN??2?140N0011?230NNNNN001?101001 3 02001210000 20100 N NN0 N 0NN201010 0??
DI	Halysiocrinus	carinatus	90	2000000?0?0NN??2140N0012231NNNNN001?101001 3 02001210000 20100 N NN0 N 0NN20101 00??
DI	Synbathocrinus	michiganensis	52	2000000?01??2????215111000N2?70N500032207500001 5 00000NNN00020100 N NN0 N 0NN301010 0??

Upper Devonian

	Genus	species	refs	data
DB	Pterinocrinus	quinquenodus	37	2010000?0?0NN??215111000N2500N50111?1?500 1101 10 0210110N00000101 N 111 2 0NN20??????
MO	Lenneocrinus	ventanillensis	16	2010000?01??2?NN??215111000N230NNNNN1?1?500 1111 10 0010120N1NN10201 N 111 ? 0NN20??????
MO	Trichotocrinus	lutheri	37	2010000?0?0NN??215111000N24 1NNNNN011?201111 10 0020121010NN00101 N 111 2 0NN?0??????
FL	Dactylocrinus	oligoptilus	89	2000000?01?????215121000N2310N5100101511001 10 00000121100000101 N 110 N 0NN20??????
FL	Eutaxocrinus	ithacensis	89	2???000?0?0NN??2150N101112310N5001?00500001 5 0010120N01000101 N 0N0 N 0NN?0??????
FL	Paralidochirus	schultzi	117	2010006?0?0NN??215111000N2500N5012111?501001 3 00100NNN00030100 N NN1 N 0NN?0??????
CL	Catactocrinus	leptodactylus	37	2010000?0?0NN??215111000N2500N50131?1?501001 5 0010100NNN00030100 N NN1 1 0NN301?110??
CL	Corematocrinus	plumosus	37	2110000?0?0NN??215?1?1000N2500N502?11?500001 5 0010121000020100 N NN0 N 0NN30???????
CL	Cradeocrinus	elongatus	37	2010006?0?0NN??215111000N2500N5012107?501001 5 0010121000020100 N NN1 1 0NN301011 0??
CL	Decadocrinus	rugistriatus	37	2010067011 0?0NN??215111000N2500N52?0N50121?501001 5 0010110N00020100 N NN1 1 0NN301011 0??
CL	Glossocrinus	naplesensis	37	2010067011 0?0NN??215111000N2500N52?0N500 11? 5 0010121100010100 N NN1 1 0NN301?1 10??
CL	Hallocrinus	ornatissimus	37	2010077010NN??215111000N2500N5012117?501001 5 00101211001 00100 N NN1 1 0NN301?110??
CL	Linobrachiocrinus	kindlei	40	2?100?0?010NN??21511001 0N2500N502312?501001 4 00000NNN00020100 N NN1 2 0NN30???????
CL	Logocrinus	infundibuliformis	37	2000000?0?0NN??215111000N2500N5012117?501001 5 0010100N00120100 N NN1 1 0NN301?110??
CL	Maragnicrinus	portlandicus	37	2?20?0?010NN??215111000N1500N5023217?501001 5 0010100N00100100 N NN1 1 0NN301?110??
CL	Prininocrinus	robustus	40	2?2?0?2??????N??2?15111000N2500N50132?501001 5 0?20120N00020100 N NN0 N 0NN30??????
CL	Pskovicrinus	sofronizkyi	81	2?2?0660?1??2?NN??2150N5011000N50112250 1001 5 0010110N00020100 N NN1 1 0NN301?110??
DI	Anamesocrinus	lutheri	37	2000000?0?0NN??2150N000013250NNNNN111?500 1001 25 20000NNN00030100 N NN0 N 0NN3010?20??

APPENDIX 3: Sources for Morphological Data on Crinoid Species

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