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BY

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# MORPHOLOGY OF CARBONIFEROUS AND PERMIAN CRINOIDS

By

MIKE FOOTE<sup>1</sup>

*Abstract*—To allow further investigation of morphological diversification in Paleozoic crinoids, this paper supplements discrete-character data on Ordovician-Devonian crinoids and presents data for Carboniferous and Permian species. In addition to 75 characters used previously, three new characters are incorporated into the data. Analysis complements previous work in suggesting that most of the spectrum of crinoid form was attained early. Morphological diversity did not continue to increase through most of the Paleozoic, even in the face of several phases of taxonomic diversification. This result further supports previous arguments for the importance of basic morphological constraints in crinoid evolution. Shifts in the distribution of morphology largely corresponded with the waning or diversification of particular higher taxa.

## INTRODUCTION

In documenting the evolutionary history of major biologic groups, data on morphological disparity are important in complementing other aspects of diversity and in leading to inferences about evolutionary mechanisms (e.g., Ward, 1980; Derstler, 1981, 1982; Saunders and Swan, 1984; Campbell and Marshall, 1987; Runnegar, 1987; Jacobs, 1990; Anstey and Pachut, 1992; Briggs et al., 1992; Foote, 1992b, 1993, 1994a,b, 1995; Sprinkle, 1992; Roy, 1994; Wagner, 1993; Smith, 1994; Wills et al., 1994). Because they have a long history marked by substantial taxonomic richness and morphological variety, a good fossil record, and a skeleton that reflects soft anatomy and function (Lane, 1963b; Brower, 1966, 1988b; Breimer, 1969; Meyer, 1973, 1979, 1983; Breimer and Webster, 1975; Breimer and Lane, 1978; Ubaghs, 1978a; Ausich, 1980, 1983, 1986, 1988; Brett, 1981; Kammer, 1985; Kammer and Ausich, 1987; Broadhead 1988a; Donovan, 1988, 1990; Riddle et al., 1988; Baumiller and Plotnick, 1989; Kendrick, 1992; Baumiller, 1990, 1993), crinoids represent an ideal clade in which to study morphologi-

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cal diversification. Although crinoids and other echinoderms may be regarded as structurally complex (Moore, 1952), this feature is no prerequisite to the investigation of disparity, which concerns variation among forms regardless of their complexity. Previous work on early and middle Paleozoic Crinoidea suggested that this clade demonstrates early morphological diversification at low taxonomic diversity (e.g., Kolata, 1975; Brower and Veinus, 1974, 1978; Sprinkle, 1982, 1990; Guensburg, 1984; Guensburg and Sprinkle, 1990, 1992; Sprinkle and Guensburg, 1991; Brower, 1992a,b, 1994; Foote, 1994a,b, 1995). Whether or not the evolutionary mechanisms underlying this pattern need be considered "special" (Gould, 1989, 1991, 1993; Briggs and Fortey, 1989; Smith 1990; Briggs et al., 1992; McShea, 1993b; Ridley, 1993; Wills et al., 1994), such early bursts of morphological diversification point toward initially accelerated rates of morphological change, or what is essentially equivalent, subsequently decelerated rates (Paul, 1977, 1979; Sprinkle, 1980, 1983, 1992; Valentine, 1986, 1991, 1992; Campbell and Marshall, 1987; Jacobs, 1990; Anstey and Pachut, 1992; Foote and Gould, 1992; Foote, 1993; Wagner, 1993; McShea, 1993b; Wills et al., 1994; but see Smith, 1990). That the level of disparity attained by crinoids in the Ordovician was not exceeded at any time through the end of the Devonian, despite striking taxonomic diversification, suggests that some basic constraints to form may have been reached early (Ausich, 1988; Foote, 1994a,b, 1995). However, the possibility remains that the apparent limits which bounded the spectrum of crinoid form were transient.

To allow analysis of morphological diversification in the later Paleozoic, this paper will supplement the set of discrete characters used previously (Foote, 1994a,b), and present morphological data for a number of Carboniferous and Permian crinoid species. Some additions and small corrections to data on Ordovician-Devonian crinoids (Foote, 1994a) will also be given. Most of these changes reflect standardization of characters following the incorporation of data on additional species. Analysis of the data will show that some morphological extremes reached before the Carboniferous were eventually surpassed to some extent. However, the evacuation of morphological space that had been occupied before the Carboniferous was at least as extensive as the colonization of new morphospace. Thus, despite renewed taxonomic and morphological diversification, the level of overall morphological diversity was no greater in the Carboniferous and Permian than it had been during the Ordovician through Devonian. Much of the evacuation and colonization of regions in morphospace reflects changes in taxonomic diversity within single higher taxa. Therefore, although homeomorphy in crinoids is common (e.g., Moore and Laudon, 1943; Sprinkle, 1980, 1983; Ausich, 1988; Broadhead, 1988a,b; Kendrick, 1992), there seems to be a fair correspondence between certain large-scale patterns of taxonomic and morphological evolution in this clade.

## MATERIALS AND METHODS

Quantification of crinoid form, sampling of species, and measurement of morphological disparity follow the methods described previously (Foote 1994a,b). A brief summary is given here.

*Crinoid Morphology.*—Because crinoids as a whole show enormous variability in the number and arrangement of skeletal plates, this paper follows previous work in using discrete (mostly binary) characters to quantify form (e.g., Lane, 1963a; Brower, 1973, 1982, 1988a; Macurda, 1974; Webster, 1981; Kammer and Ausich, 1992, 1993, 1994). The characters, chosen to be applicable to the majority of crinoid species, broadly cover four principal regions of the crinoid skeleton: the pelma (14 characters), the dorsal cup (28 characters), the arms, including fixed brachials and interbrachials (28 characters), and the anus and tegmen (8 characters). These 78 characters comprise the same 75 characters used to document morphological diversity in Ordovician-Devonian crinoids, plus three additional characters: 40A, presence of acrocrinid-

TABLE 1—Additional characters used to quantify crinoid form. Only modifications to characters in Foote (1994a: table 1) are presented here. Characters are denoted as binary (B), ordered multistate (O), or unordered multistate (U).

Character	Character description and states
<b>Pelma</b>	
1(U)	Pelma: 0, absent or directly attached. 1, multiplated holdfast. 2, column. <i>Note: State 0 incorporates state 3 of Foote (1994a).</i>
<b>Dorsal cup</b>	
<i>Note: This work follows Lane (1967) in considering the plates of Codiocrinacea having only two circlets in the dorsal cup to be basals and infrabasals.</i>	
33(U)	Shape of cup (sag.): 0, cylinder. 1, cone. 2, bowl. 3, globe. 4, inverted cone. 5, inverted bowl. 6, splayed bowl or cone (as in <i>Uperocrinus</i> ). 7, irregular. <i>Note: State 7 corresponds to state 4 of Foote (1994a).</i>
36(U)	Symmetry of cup (trans.): 0, asymmetric. 1, strongly bilateral. 2, triradial. 3, tetradial. 4, pentaradial with strong bilateral overprint. 5, pentaradial (with or without weak bilateral overprint). <i>Note: In Foote (1994a,b) states 3, 4 and 5 were presented as states 4, 5, and 6, and there was no state 3.</i>
40A(B)	Intercalary plates (as in <i>Acrocrinus</i> ): 0, absent. 1, present.
40B(O)	Number of circlets of intercalaries: state = count. <i>Note: Characters 40A and 40B were not listed in Foote (1994a). No species in Foote (1994a) is coded as having intercalary plates.</i>
<b>Arms</b>	
67A(B)	Torted arms (as in <i>Mespilocrinus</i> ): 0, absent. 1, present. <i>Note: Character 67A was not listed in Foote (1994a). No species in Foote (1994a) is coded as having torted arms.</i>

type intercalary cup plates; 40B, number of intercalary cup plates; and 67B, presence of torted arms (Table 1). These three characters were not observed to vary among the Ordovician-Devonian species initially studied (Foote, 1994a,b). Characters were coded mainly from illustrated descriptions of well preserved crinoid species in the primary literature. Species in which the arms are not preserved were omitted, but species considered to lack arms were used (Lane, 1967; see discussion below). Columnal species and other form taxa were not used. Morphological data and sources for these data are given in Appendices 1 and 2.

The homologies among crinoid plates are uncertain (e.g., Moore, 1962; Warn, 1975; Kelly, 1982; Broadhead, 1988a,b; Simms, 1993). However, because this research seeks to investigate the overall spectrum of realized forms, it is appropriate to code characters based on the topological arrangement of plates. For example, in a recent reinterpretation of crinoid plate homologies, Simms (1993; see also Kelly, 1982; Broadhead, 1988b) suggests that the arms, which are conventionally regarded as supported by radial plates (which by implication are homologous) in all crinoids (Moore, 1962), are sometimes supported by the radials, sometimes by basals, and sometimes by both on the same individual. As far as understanding how the major groups of crinoids are related, it is essential that we know whether Simms' view, the conventional view, or some other view is correct. But, regardless of whether what we conventionally call *radials* share a common evolutionary origin, they play essentially the same role structurally in the vast majority of crinoids, and for analysis of overall crinoid form it is reasonable to consider them the same element in the various crinoid taxa (see Foote 1995).

**Time Scale and Sampling.**—Stratigraphic intervals, based mainly on Harland et al. (1990), were chosen to be fine enough to give resolution of evolutionary sequences, but coarse enough to allow reasonably large sample sizes (Table 2). The Carboniferous and Permian intervals

TABLE 2—Carboniferous-Permian time scale, generic richness, and sample sizes. Totals for generic richness include genera of uncertain affinities. Ages (Ma) and durations (m.y.) from Harland et al. (1990). Corresponding information for Ordovician-Devonian intervals can be found in Foote (1994a,b). Note that most higher taxa during most intervals are sampled in proportion to their known generic diversity; exceptions are discussed in the text.

Stratigraphic interval	Age (base)	Duration	Number of genera					Total
			Mono-bathrida	Diplo-bathrida	Dispar-ida	Clad-ida	Flexi-bilia	
Tournaisian (T)	363	13	51	3	9	63	13	141
Visean (V)	350	17	43	3	8	88	15	160
Serpukhovian (Sr)	333	10	15	--	4	58	4	81
Bashkirian (B)	323	12	13	--	6	62	6	87
Moscovian (M)	311	8	14	--	6	103	6	129
Stephanian (St)	303	13	6	--	4	99	6	117
Permian-1 (P1)	290	21	5	--	5	57	4	73
Permian-2 (P2)	269	13	11	--	11	86	12	121
Permian-3 (P3)	256	11	4	--	1	13	3	21
			Number of species sampled					
Tournaisian (T)	363	13	30	3	5	24	9	71
Visean (V)	350	17	17	1	4	49	10	81
Serpukhovian (Sr)	333	10	3	--	0	25	3	31
Bashkirian (B)	323	12	0	--	0	9	0	9
Moscovian (M)	311	8	0	--	0	31	2	33
Stephanian (St)	303	13	1	--	1	31	1	34
Permian-1 (P1)	290	21	1	--	1	15	3	20
Permian-2 (P2)	269	13	3	--	4	28	8	43
Permian-3 (P3)	256	11	1	--	0	3	1	5

used are: (1) Tournaisian, including the North American sequence through the Burlington Limestone and equivalents; (2) Visean, including the North American sequence from the Keokuk and equivalents roughly through the Gasperian; (3) Serpukhovian, including roughly Hombergian through Elvirian strata; (4) Bashkirian, assumed roughly equivalent to Morrowan; (5) Moscovian, assumed roughly equivalent to Atokan and Desmoinesian; (6) Stephanian, assumed roughly equivalent to Missourian and Virgilian; (7) Permian-1, including Asselian, Sakmarian, and Wolfcampian; (8) Permian-2, including Artinskian and Kungurian; and (9) Permian-3, including the remainder of the Permian. The mean interval length for the Carboniferous and Permian is 13.1 m.y. (SD = 3.8 m.y.) (cf. subdivision of pre-Carboniferous, mean = 16.4 m.y., SD = 8.5 m.y. [Foote, 1994a,b]). Although the rich faunas from Timor (e.g., Wanner, 1916, 1924; Springer, 1924) have traditionally been considered as Upper Permian, I have followed recent evidence (e.g., Webster, 1987, 1990; Webster and Jell, 1992) that they may be closer to Artinskian (Permian-2) in age. Peter Holterhoff (personal communication, 1994) has kindly pointed out that, contrary to my assumption, the Wolfcampian-Leonardian boundary may in fact lie above the Sakmarian-Artinskian boundary. However, most (15 of 17) of the North American Wolfcampian species in the data come from the middle Wolfcampian, and therefore should be within the Permian-1 interval. The effect of uncertainties in the stratigraphic placement of Permian species will be discussed below.

Publications describing crinoid species were identified using several bibliographies, especially Webster (1969, 1977, 1986, 1988, 1993), Moore and Teichert (1978), and the *Zoological Record*, and species were chosen from these publications. In effect, all genera found by the sampling procedure and represented by relatively complete crowns were used. No more than one species per genus was sampled in any time interval. When numerous species were available, an effort was made to sample the most completely preserved representative of the genus. Restricting sampling in this way is meant to keep the study tractable, to emphasize disparity at the large scale of crinoids as a whole, and to reduce the effects of variable species concepts (Foote, 1994a,b). Although discrete characters were coded for the representative species, not the genus as a whole, the method of sampling effectively uses the genus as the basic sampling unit. This is reasonable in light of the observation that crinoid genera seem to be rather coherent units of morphology (Kammer and Ausich, 1992, 1993, 1994; see Allmon, 1992). Previously, there were two instances in which I inadvertently included two species from a single genus within a stratigraphic interval (Foote, 1994a). Although this oversight had little effect on patterns of morphological diversity, these extra species have since been removed from the Ordovician-Devonian data. In addition, eight more Ordovician-Devonian species were coded (Appendix 1). Sample sizes for the nine Ordovician-Devonian intervals are now 5, 34, 31, 19, 42, 27, 43, 42, and 18. Although there is now one more species (Sprinkle and Wahlman, 1994) representing the Lower Ordovician, many more newly discovered species remain to be described (Guensburg and Sprinkle, 1990; Sprinkle and Guensburg, 1991; T. E. Guensburg, personal communication, 1994). Therefore, future measures of disparity for this interval may be higher than current estimates.

The sample of species is large enough and sufficiently representative of the diversity of Paleozoic crinoids that the history of morphological disparity can be reasonably documented, although not without some limitations. On the whole, 50% of all recognized Paleozoic genera are represented by morphological data in this study, and the vast majority of those genera not included are known from relatively incomplete material. Moreover, the major higher taxa of crinoids are generally represented in the morphological sample in proportion to their known diversity (Table 2). However, there are some noteworthy exceptions: (1) The Serpukhovian sample contains no disparids; (2) the Bashkirian sample contains only cladids; and (3) the Moscovian sample contains no monobathrids or disparids. These shortcomings reflect the dearth of relatively complete crowns from intervals in which isolated cups are quite common (e.g., Moore and Plummer, 1938, 1940; Knapp, 1969; Moore and Strimple, 1973). Because morphological diversity reflects differences among and within groups, the absence of some groups, which occupy largely different regions in morphological space (see below), is likely to bias estimates of disparity downward. This bias is explored more elsewhere (Foote 1995), and will be touched upon below.

*Morphological Disparity.*—Metrics of disparity convey the magnitude of morphological differences among species (Wills et al., 1994). Morphological disparity within a stratigraphic interval is measured here as the mean pairwise character difference between species (normalized by the number of characters compared) (Sneath and Sokal, 1973; Cherry et al., 1982; Foote, 1992, 1994a,b; Wills et al., 1994). Calculation of character differences follows Foote (1994a: Appendix 1). Without a reasonable way to assign character weights differentially, I have adopted the standard practice of giving all characters equal weight (Sneath and Sokal, 1973). Although equal weighting is in a sense as arbitrary as any other scheme of weighting, it was shown previously (Foote, 1994a) that large-scale patterns of morphological diversity such as those documented here are unlikely to reflect the peculiarities of character weighting. This point will be explored further below.

It has been suggested (e.g., Smith, 1994) that the *total* amount of evolutionary change (including reversal), rather than *net* differences among lineages, should be the focus of studies of morphological diversity. When Smith (1994) states that phenetic distance confounds convergence with homology and underestimates the amount of morphological change that has

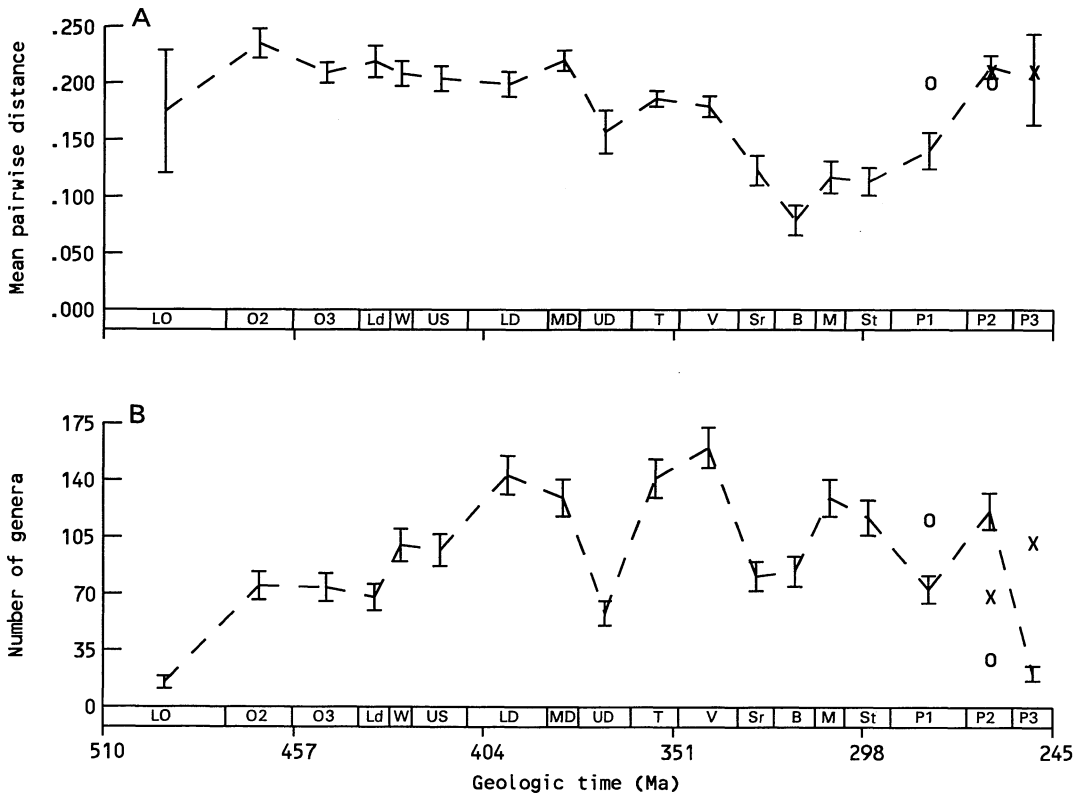


FIG. 1—Morphological disparity and taxonomic diversity in Paleozoic crinoids. A, Mean pairwise distance between species. Error bars in this and subsequent figures show 1 SE on either side of disparity estimate and are based on bootstrap resampling of data (Efron, 1982; see Foote, 1994b for interpretation of error bars). B, Generic richness (total number of described genera, not the number sampled for this study). Error bars estimated as  $\pm\sqrt{\text{number of genera}}$  (see Sepkoski and Raup, 1986; Foote, 1994b). Abbreviations for Ordovician-Devonian intervals: LO, Lower Ordovician; O2, Ordovician-2; O3, Ordovician-3; Ld, Llandoveryan; W, Wenlockian; US, Upper Silurian; LD, Lower Devonian; MD, Middle Devonian; UD, Upper Devonian. Abbreviations for Carboniferous and Permian intervals as in Table 2. Xs in Permian-2 and Permian-3 show the values disparity and diversity would have if species from Timor were assigned to Permian-3 rather than Permian-2. Os in Permian-1 and Permian-2 show the values disparity and diversity would have if species from Timor and from the Australian Callytharra Formation were assigned to Permian-1 rather than Permian-2. Despite expansions of disparity in Lower Carboniferous and Permian, maximal disparity in Paleozoic crinoids had been reached long before the time of maximal diversity. It is suggested in the text that the low disparity in the Serpukhovian through Permian-1 may be exaggerated by poor sampling (see Table 2, Fig. 2).

occurred, he seems to imply, incorrectly, that distance-based measures of disparity are intended to measure total character change. Just as taxonomic turnover (analogous to total character change) and standing diversity (analogous to disparity) reflect different aspects of taxonomic diversification, so do total change and net change reflect different aspects of morphological diversification. Neither is more fundamental than the other; they are complementary. For example, the discordance between abundant total character change (documented, even if not



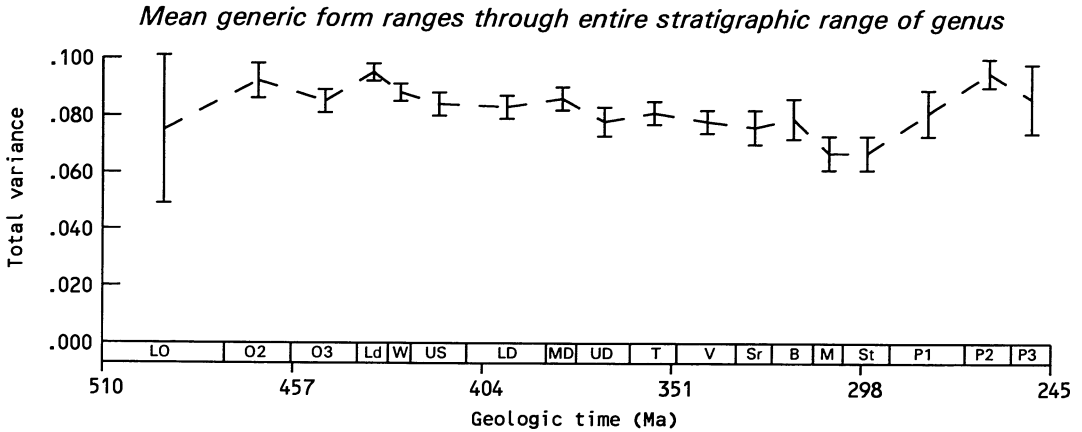


FIG. 2—Total variance (sum of univariate variances; Van Valen 1974) of first twenty principal-coordinates, with average generic morphology ranging through all stratigraphic intervals between first and last occurrence of a genus. Curve shows much less variable disparity than in raw data. In particular, comparison with Figure 1 suggests that low disparity in the raw data for the Serpukhovian through Permian-1 may be exaggerated by poor sampling (see Table 2). Sum of first twenty eigenvalues is equal to 86% of trace of distance matrix.

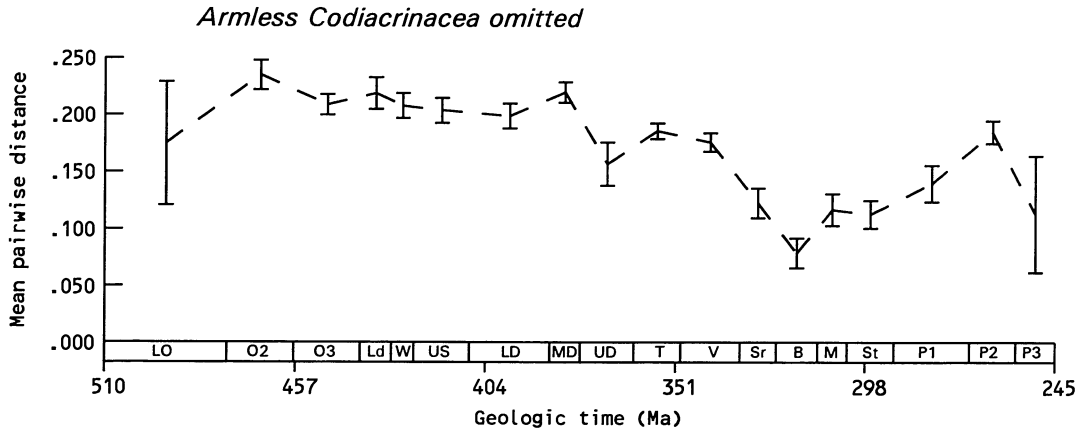


FIG. 3—Morphological disparity with armless codiacrinacean species omitted. Note drop in disparity, relative to Figure 1, in Permian-2 and Permian-3.

fully quantitatively, by over a century of studies revealing abundant morphological evolution and the origins of hundreds of new genera over the Paleozoic) and limited net change (supported by the failure of overall disparity to increase over most of the Paleozoic) provides one line of evidence for the importance of morphological constraints in crinoid evolution (Ausich, 1988; Lee 1992; Foote, 1994a,b, 1995). Insistence on the exclusive value of one aspect of diversity or diversification can hinder the insight that comes from considering many perspectives (Gould, 1991; Hickman, 1993a,b).

## ANALYSES AND RESULTS

*Diversity and Disparity.*—To compare disparity with taxonomic diversity, stratigraphic ranges of crinoid genera were compiled, based primarily on the bibliographies of Webster (1969, 1977, 1986, 1988, 1993). The compilation is described in more detail elsewhere (Foote, 1994b). Figure 1 compares generic richness with morphological disparity over the Paleozoic. The temporal patterns for the Ordovician-Devonian have not been substantially altered by the minor changes made to the data for these intervals, and therefore will not be discussed at length here (see Foote, 1994a,b). Extensive taxonomic diversification in the Lower Carboniferous corresponds with an increase in morphological diversity above the level of the Upper Devonian, but Carboniferous diversification did not result in the high level of disparity that had been achieved in the mid Ordovician. Low disparity immediately after the Visean is perhaps to be expected, following the final extinction of diplobathrid camerates. However, it is suggested below that this low level of disparity is exaggerated by biased sampling. Morphological diversity appears to increase between the Upper Carboniferous and the Upper Permian.

By allowing genera that were extant but not sampled for a stratigraphic interval to be represented in the morphological data for that interval, it is possible to take some steps toward compensating for poor sampling in the Serpukhovian through Moscovian. All species were first ordinated using principal coordinates (Gower, 1966). Treating these coordinates as continuous variables, the average form of each genus (mean form of all species in the genus) was computed, and a generic morphology was allowed to range through intervals during which the genus was extant but not sampled (see Foote, 1991, 1993, 1994b, 1995). The result of this procedure is a much flatter morphological diversity curve (Fig. 2). This result may be partly a taxonomic artifact, if unrelated homeomorphs separated by great spans of time are assigned to the same genus. However, it at least suggests that morphological disparity in the Serpukhovian through Permian-1, while it was probably higher than shown in Figure 1, was not higher than in the Tournaisian, Visean, or Permian-2.

The maximal level of morphological diversity after the Devonian is shown by the Permian-2 sample. This interval includes the diverse faunas from Timor (e.g., Wanner, 1916, 1924), which contain many forms one might be tempted to regard as unusual or "bizarre" (e.g., Springer, 1926: p. 93). Of course, there is no necessary correspondence between what we perceive as strange and what is morphologically extreme in some quantitative scheme. Nonetheless, it is worth asking to what extent the high disparity in the Permian-2 sample reflects only the 23 Timor species. If these species were assigned to Permian-3 rather than Permian-2, there would be little difference in the estimates of disparity for either of these intervals (Fig. 1). This stands in contrast to the blastoid record, where estimates of disparity in the Permian rest heavily on the Timor faunas (Foote, 1991, 1993). At the same time, it is possible that the Timor species, as well as the three species from Callytharra Formation of Australia, should be assigned a Permian-1 age (P. Holterhoff, personal communication, 1994). Accepting such an assignment would yield a substantially higher estimate of Early Permian morphological disparity (Fig. 1), implying a more rapid diversification of morphology in the Permian.

This study includes armless forms of the cyathocrine cladid superfamily Codiocrinacea. In contrast to many armless disparids that appear to represent early growth stages of arm-bearing adults (e.g., Koenig, 1965; Lane, 1967; Lane and Sevastopulo, 1981, 1982a,b, 1985), the armless forms included here have not been traced to brachiote adult forms (Lane, 1967). Nevertheless, the possibility remains (Broadhead, 1988a) that at least some of these forms are juvenile stages. The effect of including armless codiacrinaceans can be assessed if we take the extreme position that all abrachiote species should be omitted as juvenile stages. Doing so

yields lower disparity in Permian-2 and especially Permian-3 (Fig. 3). Therefore, part of the temporal pattern of disparity is rather sensitive to the status of these unusual forms.

*Morphological Distribution of Higher Taxa.*—Based on principal-coordinates analysis, the major higher taxa of crinoids occupy reasonably distinct regions in morphological space (Fig. 4) (see also Lane, 1963b; Ausich, 1980). As found previously (Foote, 1994a), the Flexibilia overlap with the other higher taxa. Within Monobathrida (Fig. 5), Compsocrinina and Glyptocrinina are somewhat distinct; this is implicit in Ubahgs' (1978b) statement that no transitional forms are known between these taxa. Within Compsocrinina, Permo-Carboniferous Hexacrinitacea are reasonably distinct from Carpocrinacea and Periechocrinacea along axis 2. Within Permo-Carboniferous Hexacrinitacea (Fig. 6), Acrocrinidae, Camptocrininae, and Dichocrininae are not mutually distinct, reflecting the unity of structure of these taxa (Wachsmuth and Springer, 1897; Springer, 1926; Moore and Strimple, 1969; Broadhead, 1981, 1985). Characters were not chosen specifically to reflect structural complexity. Because the intercalary plates that make acrocrinids appear complex account for only two out of 78 characters, structurally simple dichocrinids (Broadhead, 1981, 1985) and structurally complex acrocrinids (Moore and Strimple, 1969) do not differ greatly in form as quantified here. Within Flexibilia (Fig. 7), Permo-Carboniferous Lecanocrinacea are separate from other taxa along the second axis. Otherwise, the flexible subtaxa overlap extensively (Springer, 1920: p. 76). As for pre-Carboniferous flexibles, Permo-Carboniferous Sagenocrinida are more dispersed than Taxocrinida. This agrees with Springer's (1920: p. 116) assessment of the Taxocrinida as rather homogeneous. In addition, Lecanocrinacea are quite variable morphologically. Within Cladida (Fig. 8), Cyathocrinina and Poteriocrinina are reasonably distinct, as are Cyathocrinitacea and Codiocrinacea within Cyathocrinina. The overlap between Dendrocrinina and Poteriocrinina is perhaps to be expected, since these two suborders share many defining characters (Kammer and Ausich 1992). Within post-Devonian Poteriocrinina (Fig. 9), the various superfamilies overlap extensively, although Scytalocrinacea seem coherent along axes 1 and 3. Disparida in the Carboniferous and Permian show less diversity and morphological dispersion than they had before the Carboniferous (Fig. 10).

*Changes in Morphospace Occupation.*—That morphological disparity did not increase between the Ordovician and Permian may suggest that major constraints on crinoid form were reached early (Ausich, 1988; Foote, 1994a,b). However, it is possible for morphological distributions to evolve without a corresponding change in disparity. A single comparison between pre-Carboniferous and post-Devonian distributions gives poor resolution, but it does show some of the major features of crinoid evolution. Much of the morphological space occupied before the Carboniferous by Monobathrida (primarily Glyptocrinina) (Fig. 5), Dendrocrinina (Fig. 8), Disparida (primarily Cincinnaticrinacea and Homocrinacea) (Fig. 10), and Diplobathrida (Fig. 11), had been evacuated by the Carboniferous. The main areas of post-Devonian expansion seen in Figures 4-10 correspond with the diversification of the poteriocrine cladids (coinciding with environmental expansion; Lane 1971), and the armless codiocrinaceans (Fig. 8). In addition, on higher principal-coordinate axes there are new extremes colonized by the monobathrid superfamily Hexacrinitacea (especially Acrocrinidae, Camptocrininae, and Dichocrininae) and a few Carboniferous Flexibilia (Fig. 12). Thus, much of the occupation of new morphological space coincides with the diversification of particular higher taxa (Lane, 1967; Moore and Strimple, 1969; Broadhead, 1981, 1985).

Apparent changes in morphological distribution illustrate a limitation of empirical morphospaces (Raup, 1966, 1967; Gould, 1991; McGhee, 1991). A large group of very similar species has the potential to "pull" the axes because of its sheer numbers. To investigate this possibility, a culling procedure (described in detail in Foote, 1995) was used to thin down the samples so that each genus would be separated from all other contemporaneous genera by a morphological distance at least as great as the median distance among congeneric species. Recomputed principal coordinates based on the culled data show that many pre-Carboniferous Dendrocrinina, Glyptocrinina, Disparida, Rhodocrinitacea, and some Flexibilia occupy regions

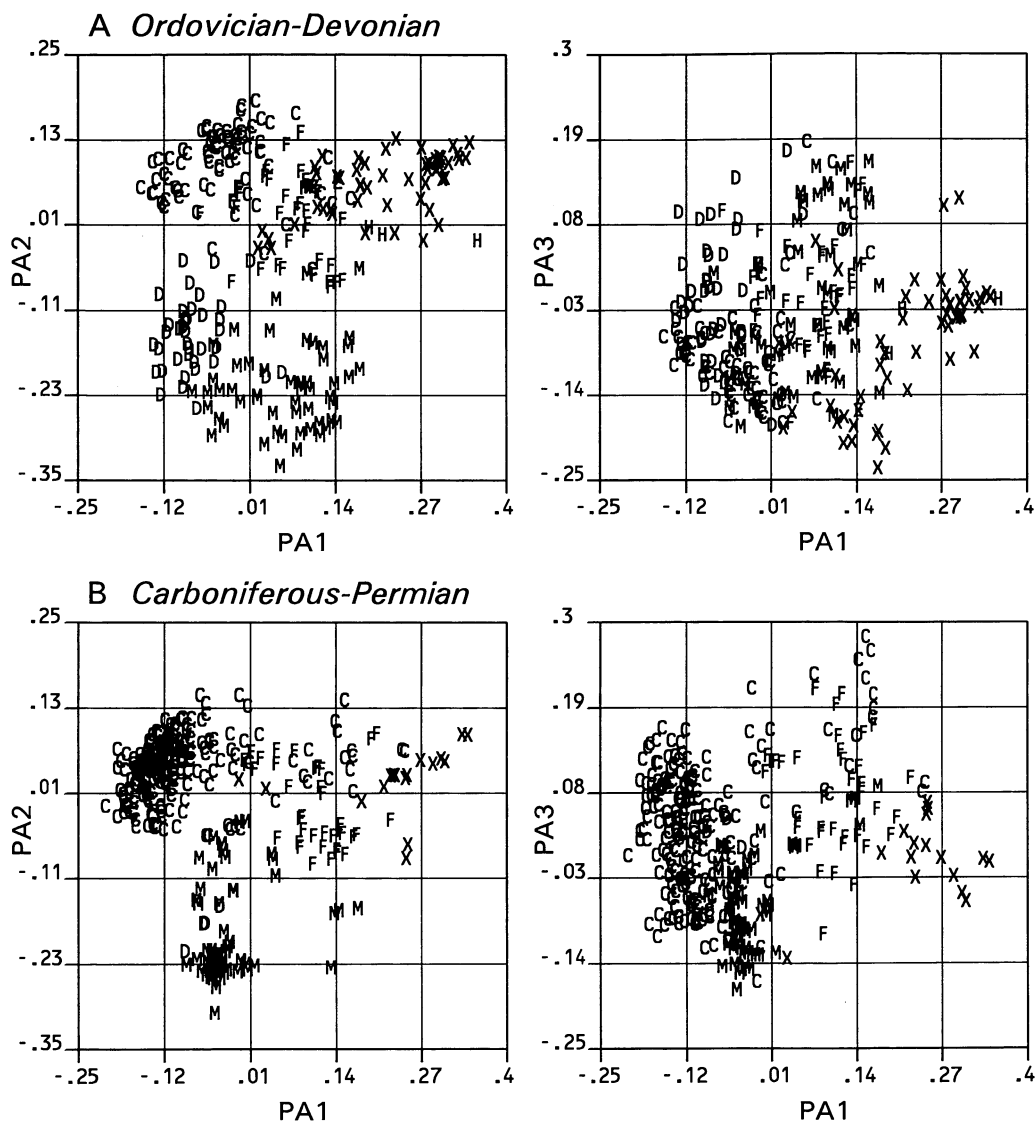


FIG. 4—Distribution of higher taxa along first three principal-coordinate axes. A, Ordovician-Devonian; B, Carboniferous and Permian. Key: C, Cladida; D, Diplobathrida; F, Flexibilia; H, Hybocrinida; M, Monobathrida; X, Disparida. Compare with Figures 5-11. Areas in morphological space essentially evacuated before the Carboniferous and Permian include those corresponding to dendrocrine cladids, disparids (especially Homocrinacea and Cincinnaticrinacea), diplobathrids (especially Rhodocrinitacea), and certain monobathrids (Glyptocrinina). Areas in morphospace newly colonized in the Carboniferous and Permian include those corresponding to poteriocrine cladids (with low values of principal coordinate 1), and codiacrinacean cladids and some flexibles (with high values of principal coordinate 3). Sum of first three eigenvalues is equal to 38% of trace of distance matrix.

*Monobathrida*

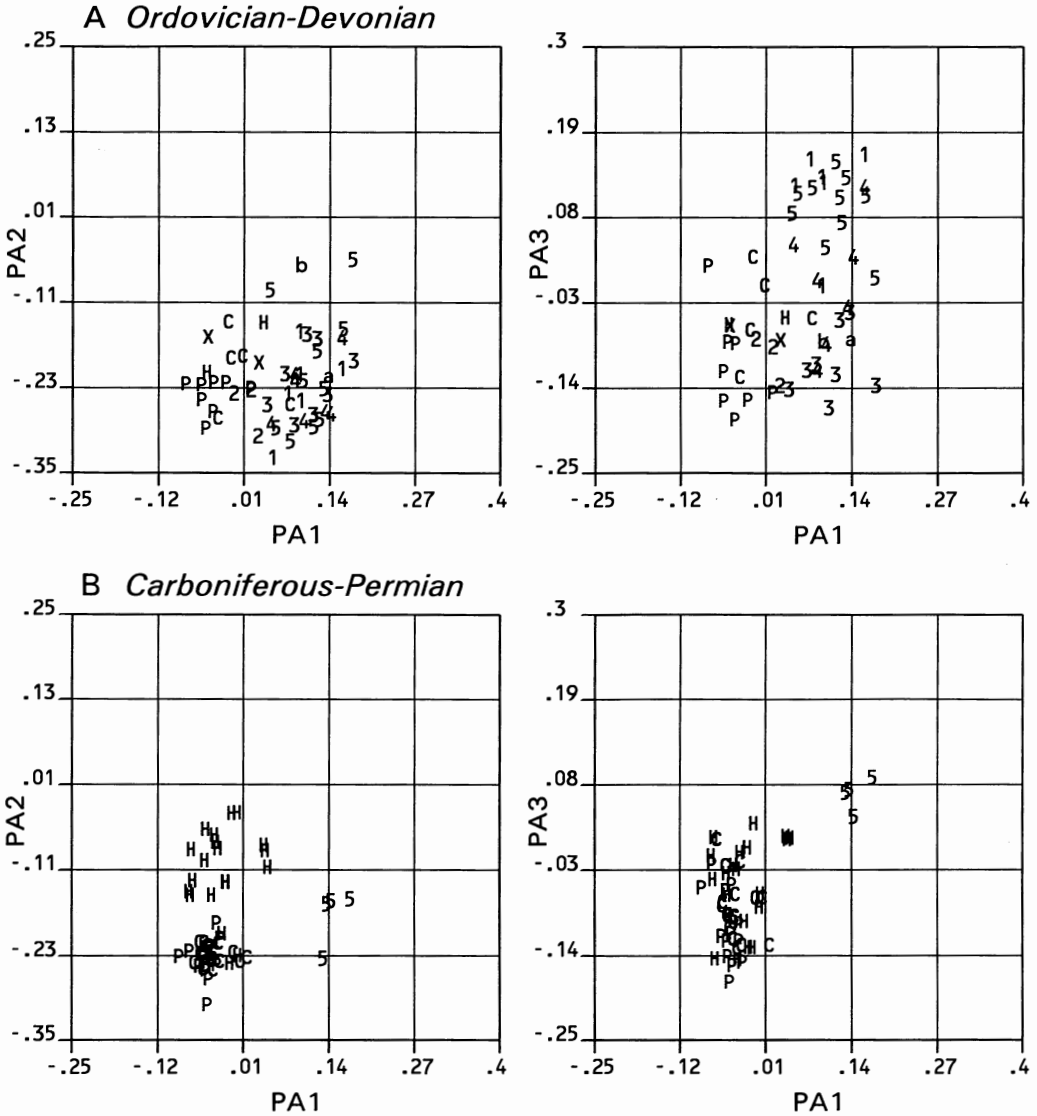


FIG. 5—Species of Monobathrida along first three principal-coordinate axes. A, Ordovician-Devonian; B, Carboniferous and Permian. Key: upper case letters, Compsocrinina (C, Carpsocrinacea; H, Hexacrinitacea; P, Periechocrinacea; X, Xenocrinacea); numerals, Glyptocrinina (1, Eucalyptocrinitacea; 2, Glyptocrinacea; 3, Melocrinitacea; 4, Patelliocrinacea; 5, Platycriniteacea); a, *Stipatocrinus*; b, *Colpodecrinus*. Note that Compsocrinina and Glyptocrinina occupy somewhat different morphological regions. Comparing pre-Carboniferous with Permo-Carboniferous, field of Compsocrinina is expanded by diversification of Hexacrinitacea, while field of Glyptocrinina is reduced by loss of all superfamilies but Platycriniteacea.

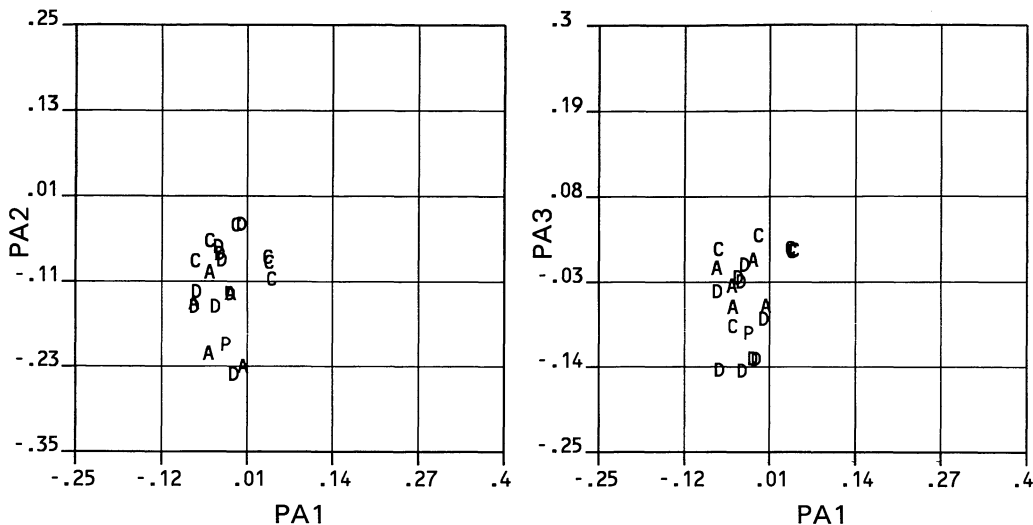
*Carboniferous-Permian Hexacrinitacea*

FIG. 6—Species of Carboniferous and Permian Hexacrinitacea along first three principal-coordinate axes. Key: A, Acrocrinidae; C, Camptocrininae (Dichocrinidae); D, Dichocrininae (Dichocrinidae); P, *Pterotocrinus* (Talarocrininae, Dichocrinidae). Families and subfamilies do not seem to occupy distinct morphological fields.

in morphological space that were not occupied in the Carboniferous and Permian (Figs. 13, 14). Newly colonized morphospace still reflects mainly the Codiocrinacea and Hexacrinitacea as before, but Poteriocrinina to a lesser extent. The expansion of morphospace corresponding with the poteriocrine radiation apparently reflects, at least in part, a pull on the principal-coordinate axes because of the sheer number of poteriocrine species, rather than their extreme morphology.

*Character Contribution to Principal-Coordinate Axes.*—Because the principal-coordinate axes do not represent all the variation in the original morphological data, it is worth asking to what extent the characters themselves are represented by the axes. As an analog to loadings in R-mode principal-components analysis, the strength of association between the discrete characters and the principal coordinates was calculated. For binary and ordered multistate characters, the gamma coefficient (Siegel and Castellan, 1988: p. 291) was used, and for unordered multistate characters the Cramér coefficient was used (Siegel and Castellan, 1988: p. 225), with the principal coordinates arbitrarily divided into four equal intervals. Although the apparent statistical significance of these associations is exaggerated by the nonindependence of species (Raup and Gould, 1974; Felsenstein, 1985), the coefficients still allow the relative strengths of association to be assessed (Table 3). About half the characters contribute substantially to one or more of the first three principal-coordinate axes, suggesting that the principal-coordinate space represents a fair proportion of the information in the larger set of characters. However, for the rest of the characters, information is spread out over many principal coordinates rather than being concentrated. It was previously shown (Foote, 1994b) that the temporal pattern of variability in the first twenty principal coordinates reflects that in the discrete characters rather well. The same is found for the revised data (result not presented here).

On the first principal-coordinate axis, higher coordinates are associated with the following features: meric stem, homeomorphic stem, fewer radials, closed radials (but radials more likely to be open by basals if open), monocyclic cup (but basals more likely to be unequal if cup di-

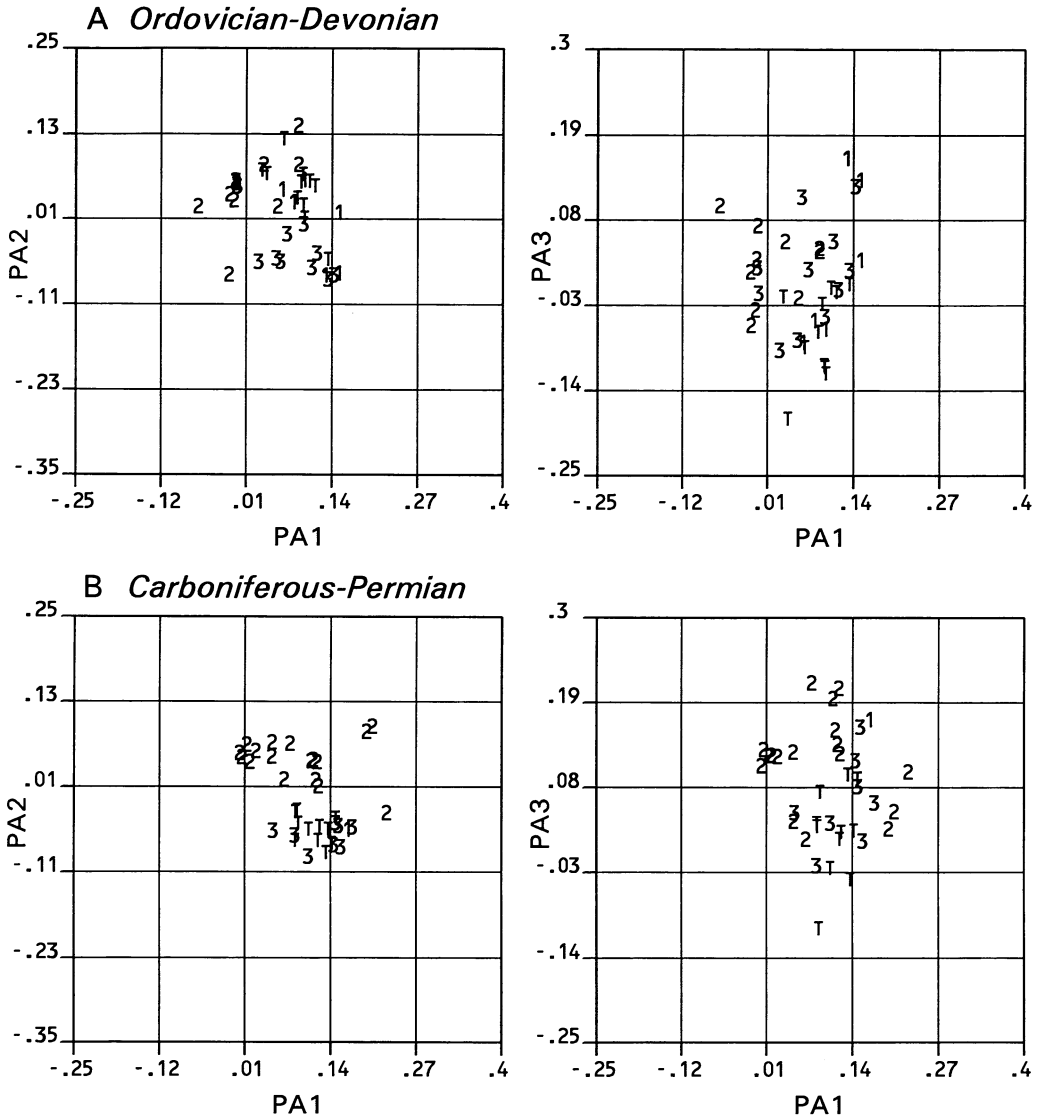
*Flexibilia*

FIG. 7—Species of *Flexibilia* along first three principal-coordinate axes. A, Ordovician-Devonian; B, Carboniferous and Permian. Key: numerals, Sagenocrinida (1, Ichthyocrinacea; 2, Lecanocrinacea; 3, Sagenocrinitacea); T, Taxocrinida. Sagenocrinida and Taxocrinida overlap extensively. Sagenocrinids are more dispersed than taxocrinids, and Lecanocrinacea is especially variable in form.

cyclic), radial prongs, unequal radials, compound radials, fewer plates in basalmost circlet, basalmost plates unequal, fewer anals in cup, higher cup, convex base, cup diminutive relative to stem, cup cylindrical or globose, cup bilateral or pentaradial without strong bilateral overprint, lack of arms, more arms when present, multiple arms on a single radial, shorter arms, unbranched arms (but greater degree of branching and more likely to be heterotomous when branched), presence of fixed brachials, lack of pinnules, symmetric uniserial brachials,

*Cladida*

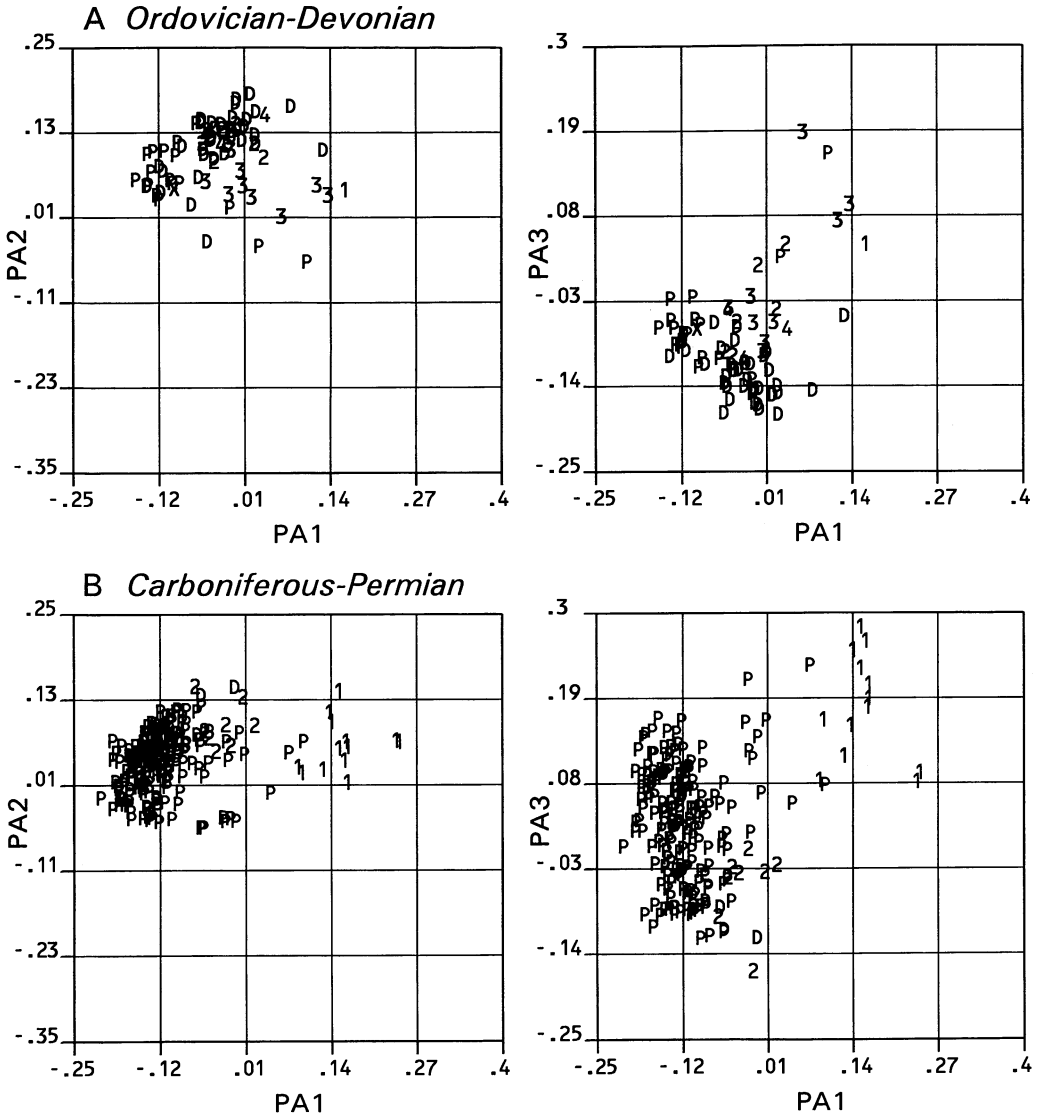


FIG. 8—Species of *Cladida* along first three principal-coordinate axes. A, Ordovician-Devonian; B, Carboniferous and Permian. Key: D, Dendrocrinina; P, Poteriocrinina; numerals, Cyathocrinina (1, Codiocrinacea; 2, Cyathocrinitacea; 3, Gasterocomacea; 4, Thalamocrinidae). Comparing A and B, note contraction in field occupied by Dendrocrinina and expansion of fields occupied by Poteriocrinina and Codiocrinacea.



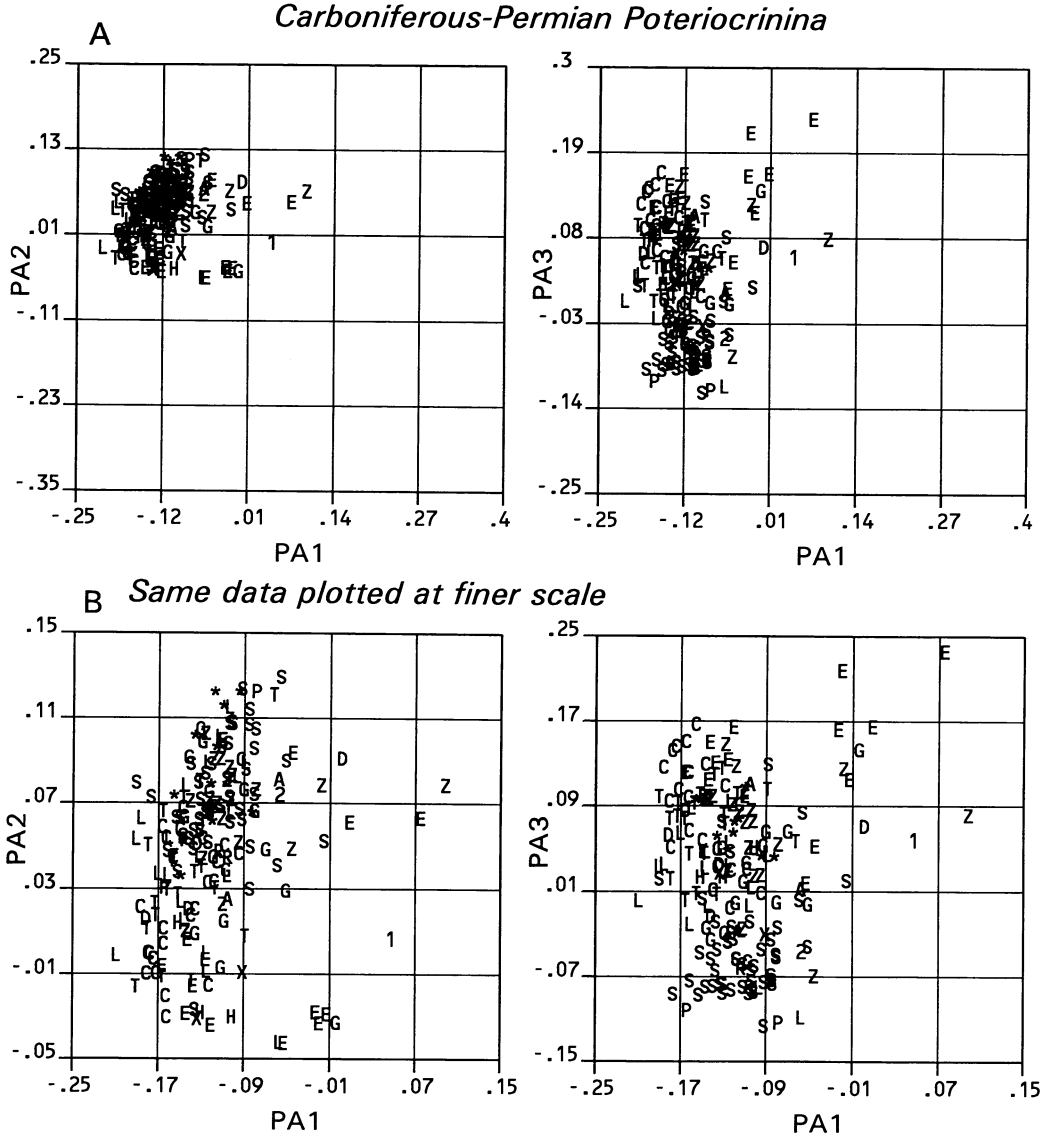


FIG. 9—Species of Carboniferous and Permian Poteriocrinina along first three principal-coordinate axes. A, data plotted at same scale as Figures 4-8 and 10-11; B, data plotted at finer scale. Key: G, Agassizocrinacea; A, Apographiocrinacea; C, Cromyocrinacea; X, Calceolispongiacea; D, Decadocrinacea; E, Erisocrinacea; H, Hydreionocrinacea; L, Lophocrinacea; I, Pirasocrinacea; P, Poteriocrinacea; R, Rhenocrinacea; S, Scytalocrinacea; T, Texacrinacea; Z, Zeacrinacea; ?, superfamily uncertain. Note that Scytalocrinacea tend to cluster together, but on the whole, superfamilies overlap extensively.

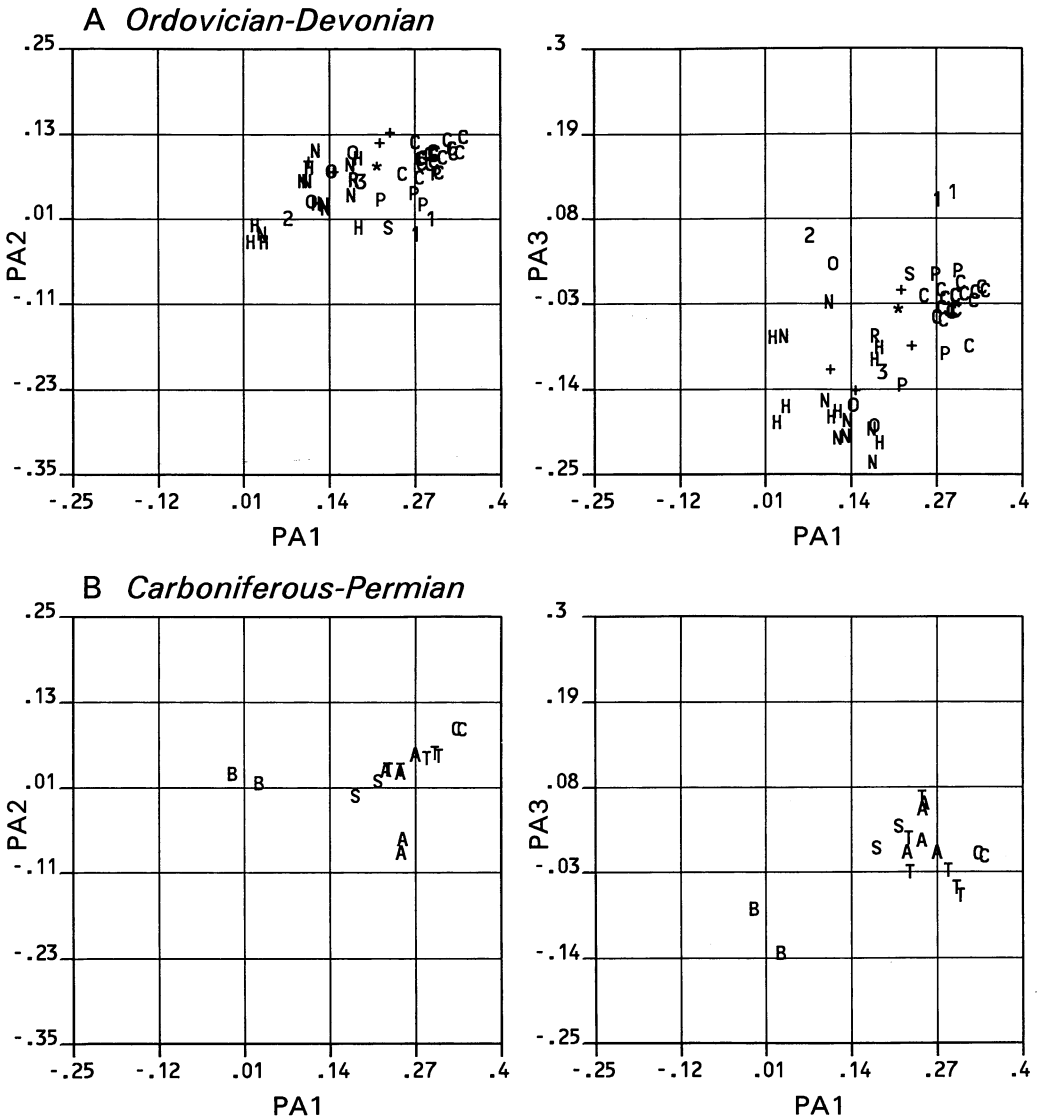
*Disparida*

FIG. 10—Species of *Disparida* along first three principal-coordinate axes. A, Ordovician-Devonian; B, Carboniferous and Permian. Key: numerals, Ordovician-Devonian Allagecrinacea (1, Acolocrinidae; 2, *Agostocrinus*; 3, Anamesocrinidae); A, Allagecrinidae (Allagecrinacea); T, Catilloocrinidae (Allagecrinacea); B, Belemnocrinidae (Belemnocrinacea); S, Synbathocrinidae (Belemnocrinacea); C, Calceocrinidae (Calceocrinacea); N, Cincinnaticrinacea; H, Homocrinidae (Homocrinacea); R, *Ramseyocrinus*; other symbols, Myelodactylacea (\*, Eustenocrinidae; O, Iocrinidae; +, Myelodactylidae). *Disparids* seem more dispersed morphologically before the Carboniferous.

*Diplobathrida*

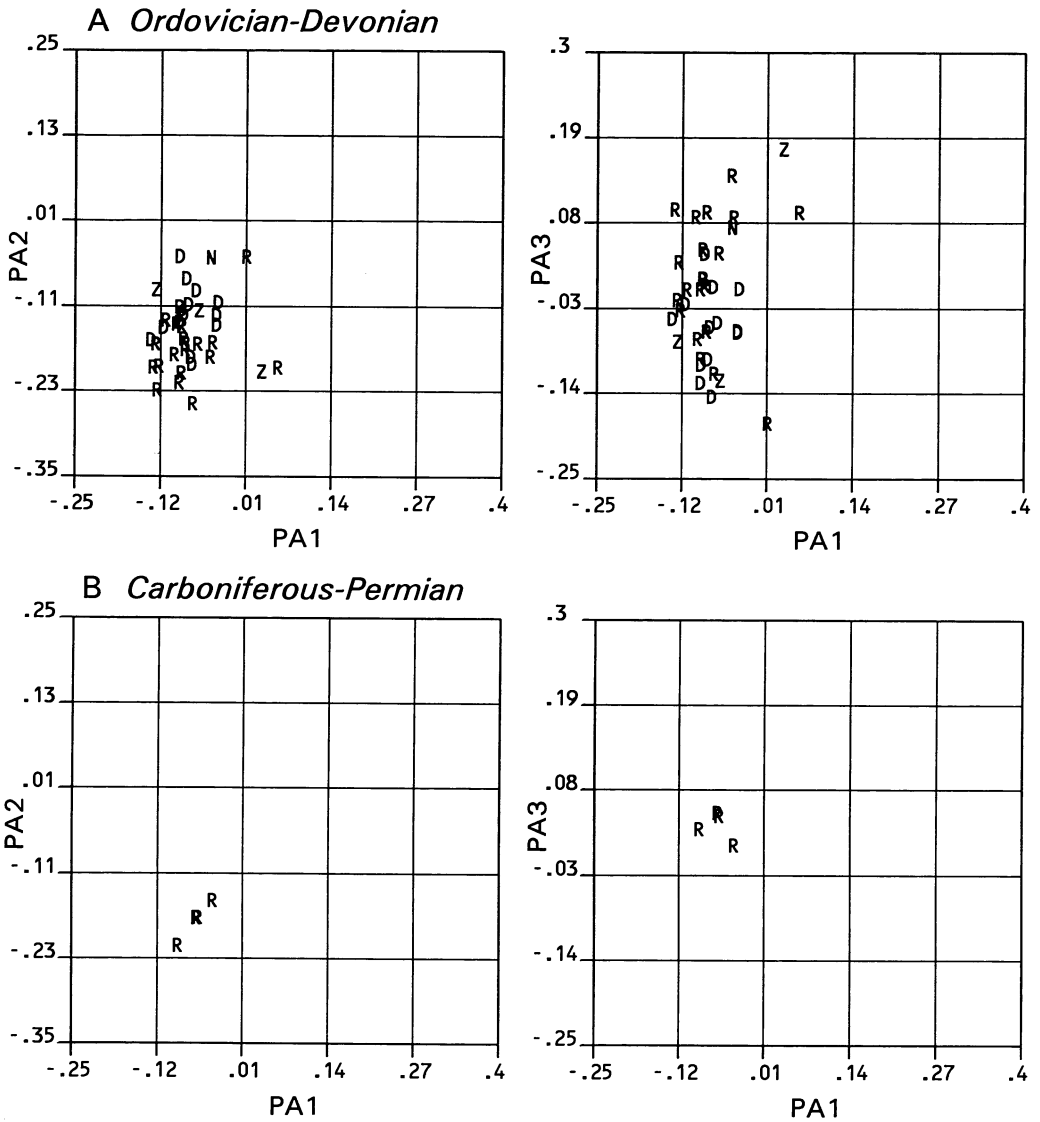
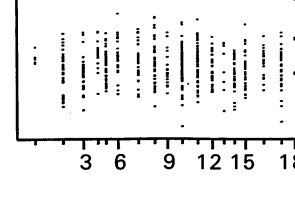
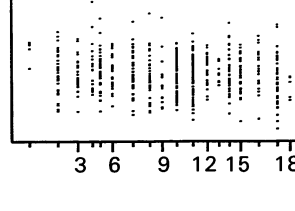
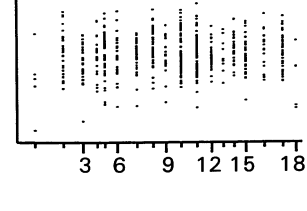
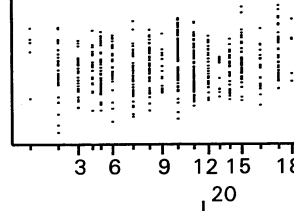
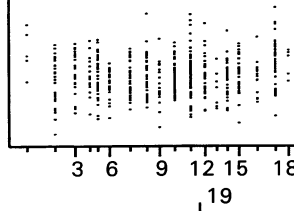
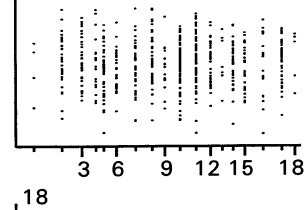
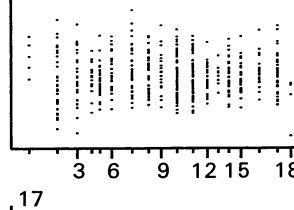
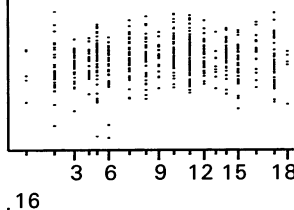
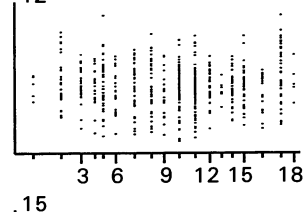
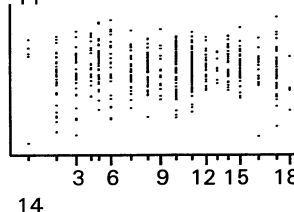
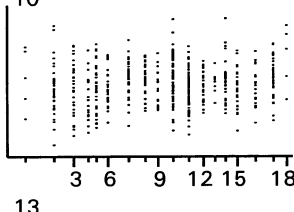
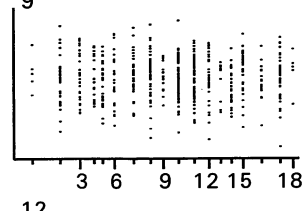
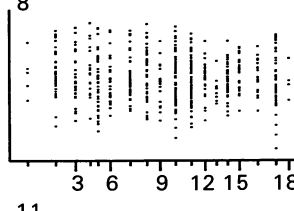
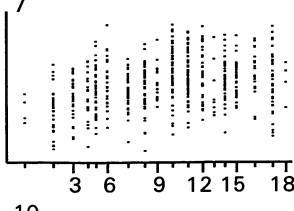
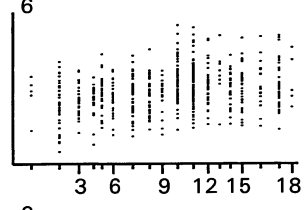
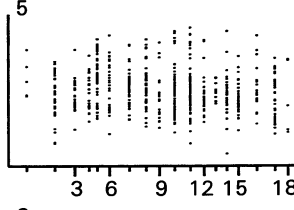
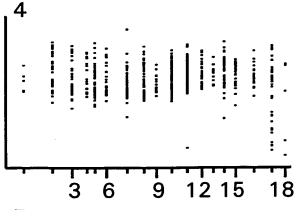
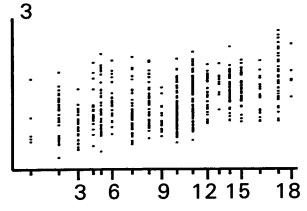
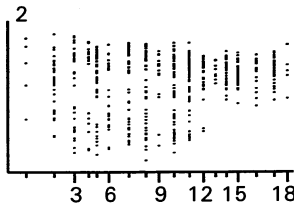
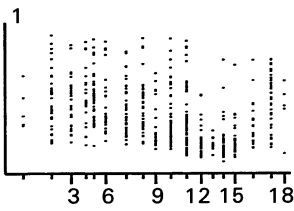


FIG. 11—Species of Diplobathrida along first three principal-coordinate axes. A, Ordovician-Devonian; B, Carboniferous and Permian. Key: D, Dimerocrinitacea; N, Nyctocrinacea; R, Rhodocrinitacea; Z, Zygodiploathrina. Comparing A and B, note great contraction in morphological field of Diplobathrida, corresponding with loss of most of the subtaxa.

Principal coordinate



Stratigraphic Interval

anus through dorsal cup, anal tube absent (but more likely to occupy posterior position and lack ridges when present), and tegmen consisting of a few plates. In addition to the obvious complements to the foregoing, lower coordinates on the first axis correspond to pentagonal and pentastellate stem, bowl-shaped cup, cup pentaradial with strong bilateral overprint, and multiplated tegmen. Axes 2 and 3 show similar associations with some of the characters (Table 3). In addition, species with elongate stem ossicles tend to have low coordinates on the third axis. Much of the pattern of association between characters and principal coordinates makes sense in terms of the positions of higher taxa along the axes (cf. Figs. 4-11, Appendix 1).

*Effect of Unknown Characters.*—In calculating a pairwise dissimilarity between species, characters that are logically applicable but whose states are unknown in either or both of the species make no contribution to the distance. The validity of this convention rests upon the assumption that, as far as morphological disparity is concerned, the missing characters are drawn from the same underlying distribution as the known characters. A disproportionately large part of the missing data reflects characters of the stem (Table 4), whose temporal pattern of disparity was shown not to match that of overall morphology (Donovan, 1986, 1989a,b; Foote, 1994b). Because nearly complete stems become far less common after the Devonian (Table 4), it is conceivable that a bias could be imparted to the pattern of disparity over the entire Paleozoic. (Tegmina are also slightly less complete on average after the Devonian [see Moore and Laudon, 1943: p. 35; Strimple, 1973], but this difference is not as great as for stems [Table 4].) The history of disparity barely changes if characters of the stem and tegmen are omitted (leaving an average of only 1-2 missing characters per species) (Fig. 15). Thus, temporal changes in the distribution of missing data do not appear greatly to bias the patterns of disparity documented here (Foote 1995).

*Variation in Character Weighting.*—As discussed above, characters were weighted equally in the calculation of morphological distances. One might reasonably ask how sensitive the temporal pattern of disparity is to the convention of equal character weighting. To explore this question, a set of random character weights was assigned and the disparity curve recomputed. This procedure was repeated 100 times to gain an idea of the range of patterns that would result from arbitrary character weighting. In order to yield a mean weight of unity, random weights were sampled from the uniform distribution on (0,2). The curves differ in height (Fig. 16), but show roughly the same pattern amongst themselves and compared to the pattern derived from equal weighting (Fig. 1). The major differences are that, with random weights, disparity is not always greatest in the mid Ordovician, and estimated disparity in Permian-3 sometimes

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FIG. 12—Ordination of Paleozoic crinoids along first twenty principal-coordinate axes. Each point represents a species. Stratigraphic intervals 1-18 correspond with Lower Ordovician through Permian-3 (see Table 2 and Fig. 1). For clarity, only every third interval is labeled. Vertical scale is not the same in all panels. Some exceedance of Carboniferous and Permian species beyond Ordovician-Devonian extremes, and of Ordovician-Devonian species beyond Carboniferous and Permian extremes can be noted, as follows. Extremely low values on axis 1 are mainly Carboniferous and Permian Poteriocrinina. Extremely high values on axis 2 are mainly Ordovician-Devonian Dendrocrinina. Extremely low values on axis 3 are mainly Ordovician-Devonian Disparida. Extremely high values on axis 3 and extremely low values on axis 4 are mainly Carboniferous and Permian Codiocrinacea. Extremely high values on axis 5 are mainly Carboniferous Flexibilia. Extremely low values on axis 6 are mainly Ordovician-Devonian Diplobathrida (primarily Rhodocrinitacea). Extremely high values on axis 6 are mainly Carboniferous and Permian Hexacrinitacea. Extremely low values on axis 7 are mainly Ordovician-Devonian Disparida and Diplobathrida (all Rhodocrinitacea). Extremely high values on axis 8 are mainly Calceocrinacea. Extreme values on remaining axes are much less homogeneous taxonomically.

TABLE 3—Patterns of association between principal coordinates and morphological characters. See table 1 and Foote (1994a) for description of characters. Binary, ordered multistate, and unordered multistate characters are denoted by B, O, and U, respectively. Symbols show relative strength of association (■ for  $p < 0.05$ , ■■ for  $p < 0.01$ , and ■■■ for  $p < 0.001$ , assuming independence of species.) For binary and ordered characters, strength of association is evaluated with gamma coefficient; sign gives direction of correlation. For unordered characters (for which association lacks direction), strength of association is evaluated with Cramér coefficient. Very few of the coefficients of association for higher axes are significant; therefore, these are not presented.

Character	Principal coordinate axis		
	Axis 1	Axis 2	Axis 3
<b>Pelma</b>			
1(U) Form of pelma			
2(B) Xenomorphy			
3(B) Heteromorphy	-■■■	-■■	
4(B) Coiled column			
5(B) Meric columnals	+■		
6(U) Shape of columnals	■■■		
7(U) Shape of lumen			
8(B) Relative height of columnals			+■
9(B) Columnal articulation			
10(B) Cirri			
11(B) Regular cirral arrangement			
12(B) Form of cirral arrangement			
13(B) Specialized distal structure			
14(U) Form of distal structure			
<b>Dorsal cup</b>			
15(B) Regular plating			
16(O) Number of radials	-■■■	-■	
17(B) Open radial cirplet	-■■■	-■■■	-■■■
18(U) Nature of opening	■■■		
19(B) Number of cirplets	-■■■	-■	
20(B) Radial prongs	+■■■	+■	
21(B) Relative development of radials	+■■■	+■■■	
22(B) Compound radials	+■■■	+■■■	
23(O) Number of compound radials			
24(O) Relative size of radial and basal-most cirplets			
25(O) Number of basal-most plates	-■■■	-■■■	-■
26(B) Relative development of basal-most plates	+■■■	+■■■	+■■■
27(B) Open intermediate cirplet			
28(U) Nature of opening			
29(O) Number of plates in intermediate cirplet			-■■■
30(B) Relative development of plates in intermediate cirplet	+■■■		
31(O) Relative size of intermediate and radial cirplets			
32(O) Number of anal plates in cup	-■■■	-■■■	-■■■
33(U) Cup shape (sag.)	■■■	■■■	■
34(O) Relative cup height			
35(U) Cup shape (trans.)			
36(U) Cup symmetry (trans.)	■■■	■■■	■■■
37(B) Concave base	-■■■		
38(B) Relative diameter of cup and stem	-■■■		
39(B) Median ray ridges			
40(B) Stellate ridges			
40A(B) Intercalary plates			
40B(O) Number of cirplets of intercalaries			

TABLE 3 (continued)

Character	Principal coordinate axis		
	Axis 1	Axis 2	Axis 3
<b>Arms</b>			
41(B) Arms present	- ■■■■	- ■■	- ■
42(O) Number of distinct arms	+ ■■		
43(O) Number of arms on single radial	+ ■■		
44(O) Relative development of arms			
45(O) Separation of arms			
46(B) Arm fusion between rays	+ ■	+ ■	
47(B) Arm branching	- ■■		
48(O) Degree of branching	+ ■		
49(B) Isotomy or heterotomy	+ ■■		
50(U) Form of heterotomy	■■■		
51(B) Uniserial or biserial plating			
52(B) Patelloid process			
53(B) Brachial asymmetry	- ■■■		
54(O) Relative brachial height			
55(B) Arm fusion within rays			
56(O) Arm attitude			
57(B) Recumbent arms			
58(B) Fixed brachials	+ ■■■		
59(O) Number of fixed brachials			
60(B) Interbrachials			
61(B) Form of interbrachials			
62(B) Pinnules	- ■■■	- ■■■	- ■
63(O) Number of pinnules per brachial			
64(B) Recumbent ambulacra			
65(O) Number of recumbent ambulacra			
66(B) Extent of recumbent ambulacra			
67(O) Ratio of arm length to cup height	- ■■■	- ■	
67B(B) Tortured arms			
<b>Anal and tegminal features</b>			
68(B) Anal opening through cup	+ ■■■	+ ■	
69(B) Anal tube or sac	- ■■		
70(O) Position of tube or sac	- ■■■		- ■
71(B) Extent of tube or sac			
72(B) Ridges on tube or sac	- ■■		
73(B) Regular plating of tube or sac			
74(B) Multiplated tegmen	- ■■■		- ■
75(B) Extent of tegmen			

*Data culled to increase separation of species*

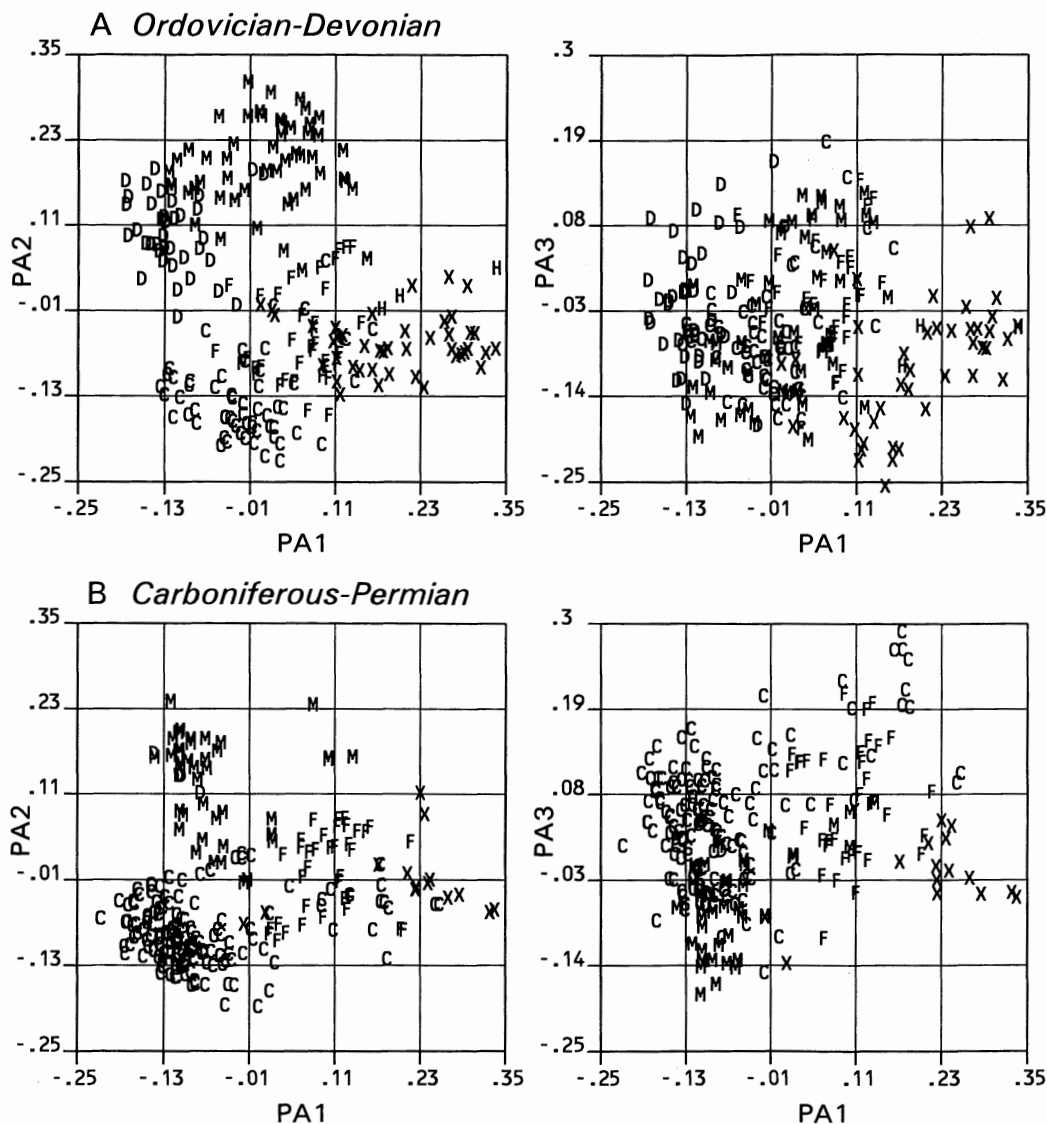


FIG. 13—Distribution of higher taxa along first three recomputed principal-coordinate axes, based on data culled to yield morphological separations among contemporaneous genera at least as great as the average separation among congeneric species. A, Ordovician-Devonian; B, Carboniferous and Permian. Key to higher taxa as in Figure 4. Higher taxa that evacuated areas in morphospace before the Carboniferous or colonized areas anew after the Devonian are largely the same as for the unculted data. The main difference is that poteriocrine cladids no longer define the extreme values of the first principal coordinate and no longer appear to represent as substantial an expansion of occupied morphological space for crinoids as a whole. This suggests that the extent to which poteriocrines expanded into new morphological space is exaggerated by the pull this clade exerts, by virtue of its sheer numbers rather than its extreme morphology, on the principal-coordinate axes (see also Figs. 4, 12, and 14).



TABLE 4—Mean number of unknown characters per species.

Stratigraphic interval	Stem	Cup	Arms	Tegmen	Total
Lower Ordovician	4.2	1.8	1.0	5.0	12.0
Ordovician-2	3.5	0.8	1.3	2.9	8.5
Ordovician-3	3.4	1.2	0.1	2.9	7.6
Llandoveryan	3.3	0.8	1.0	3.6	8.7
Wenlockian	3.9	0.5	0.1	3.7	8.2
Upper Silurian	4.9	0.9	0.1	3.1	9.0
Lower Devonian	5.5	1.0	0.5	4.1	11.1
Middle Devonian	5.4	0.5	0.4	2.8	9.1
Upper Devonian	5.2	1.4	0.4	5.0	12.0
Tournaisian	5.4	0.7	0.7	2.7	9.6
Visean	5.9	0.9	0.9	4.0	11.7
Serpukhovian	7.8	0.8	0.4	4.7	13.7
Bashkirian	9.0	1.1	1.2	6.7	18.0
Moscovian	7.9	0.6	1.2	5.2	14.9
Stephanian	6.4	0.8	1.0	5.0	13.2
Permian-1	6.1	1.2	1.4	4.9	13.5
Permian-2	8.6	0.6	2.0	3.8	14.9
Permian-3	10.0	0.5	2.0	2.8	15.2

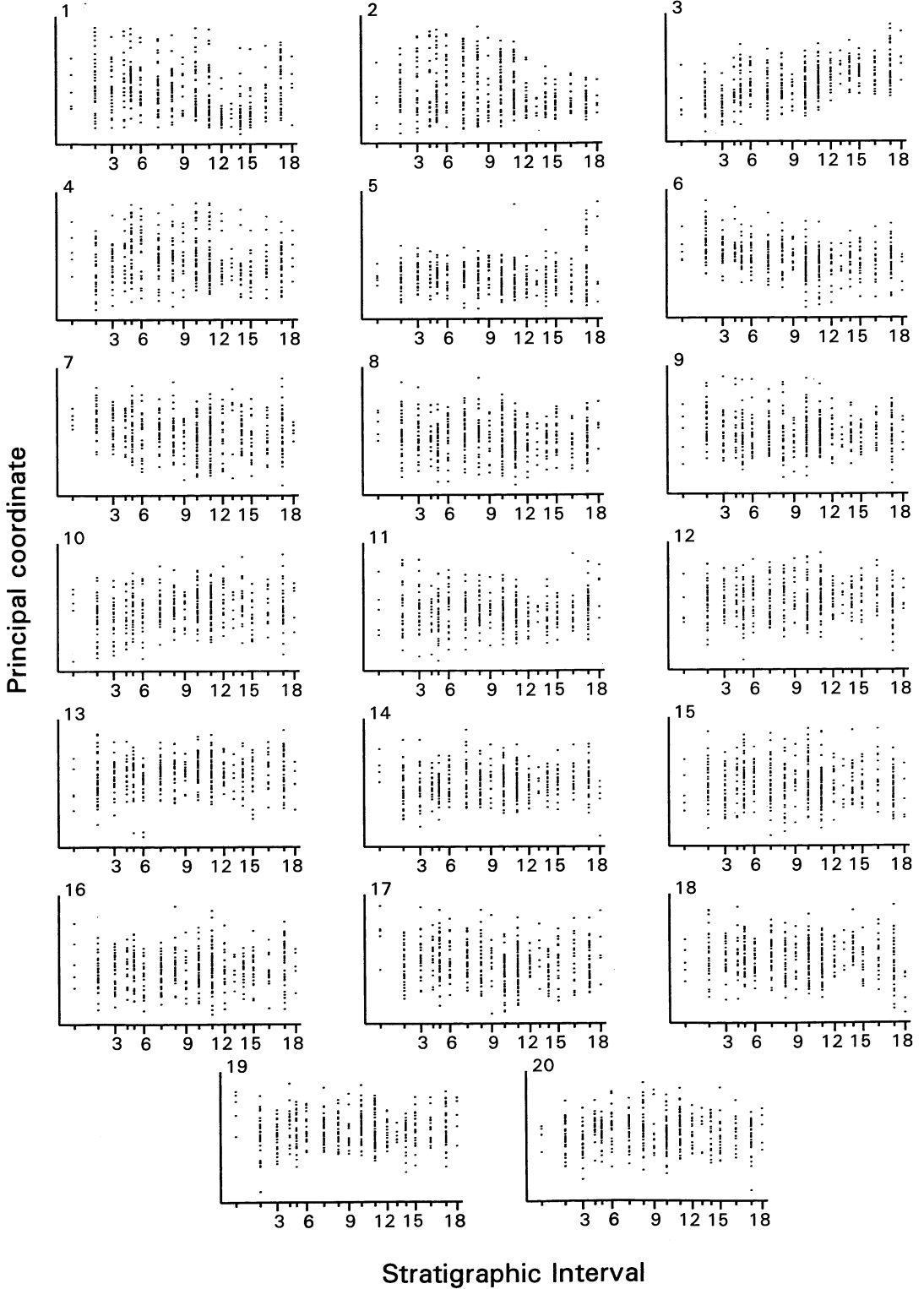
exceeds the level of the Ordovician. However, since the Permian-3 sample contains only five species, this last result should be treated with caution.

The foregoing approach allows a limited variation in character weight between 0 and 2. An alternative is to allow greater variation in weight by bootstrapping the characters, i.e. resampling the characters with replacement. In this way, a character can, in principle, be weighted between 0 and  $M$ , where  $M$  is the total number of characters, while still having an average weight of unity over a large number of character samples. This procedure results in more variation among the disparity curves (Fig. 17), but these curves still have the same general shape.

Although the decline in disparity between the Visean and Stephanian may be a sampling artifact (see above), it is reasonable to conclude that the major feature of crinoid history documented here, namely a lack of increase in disparity through most of the Paleozoic, despite extensive taxonomic diversification and some 200 million years of post-Ordovician evolution, is not an artifact of character weighting.

None of the approaches to character weighting used here attempts to assign weight to character complexes. It is probable that many characters evolve nonindependently as complexes. According to all three weighting schemes explored above, such complexes would tend to be weighted in proportion to the number of unit characters into which they are decomposed for the sake of analysis. One might want to devise a weighting scheme in which each character complex was given unit weight. However, at least partly because the concept of a character complex is so variable, we do not yet have an objective and fully general way of recognizing such complexes (see Olson and Miller, 1958, Campbell and Barwick, 1990, and Zelditch et al., 1992 for some discussions of this issue). Although much remains to be said on this subject, the fact that cup characters and arm characters alone each show sequences of disparity broadly similar to that based on all characters (Foote, 1994b) suggests that the large-scale history of disparity in crinoids does not simply reflect undue weight assigned to a small number of characters.

*Data culled to increase separation of species*



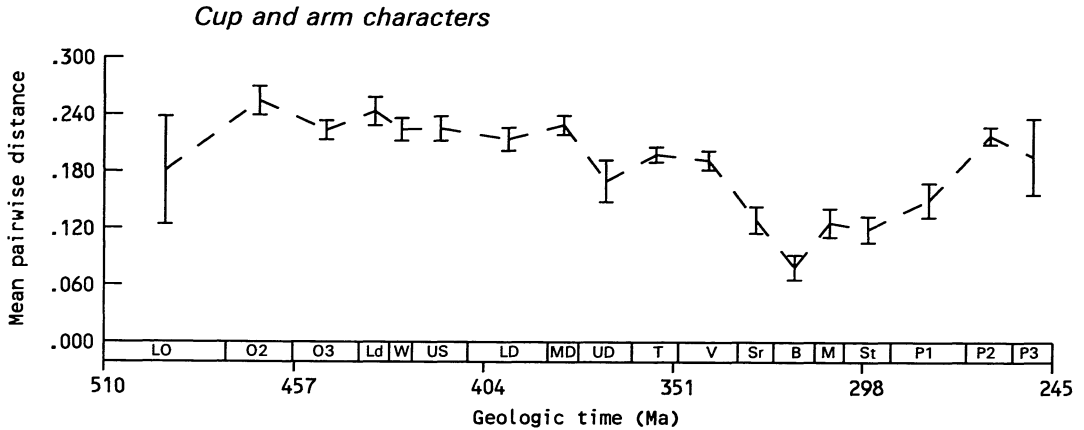


FIG. 15—Morphological disparity in Paleozoic crinoids, omitting characters of the stem and tegmen, the morphological regions that account for the majority of missing data (Table 4). Pattern is very similar to that based on all characters, suggesting that overall pattern is not an artifact of temporal changes in missing data.

#### DISCUSSION AND SUMMARY

The foregoing analyses of discrete characters complement previous work in suggesting that most of the spectrum of crinoid form evolved fairly early in the history of the clade (Ausich, 1988; Foote, 1994a,b, 1995). This result is robust, not being sensitive to character weighting or missing data. The same result is shown in a cruder way by the fact that only three of 78 characters that vary among crinoids as a whole did not vary among species in the pre-Carboniferous sample. Other aspects of the distribution of morphology are considered elsewhere (Foote 1995).

Although morphological disparity did not increase substantially after the Ordovician, the distribution of forms was not static. In addition to well noted evolutionary trends within higher taxa (e.g., Springer, 1920; Moore and Laudon, 1943; Moore, 1952; Lane and Webster, 1966;

FIG. 14—Ordination of Paleozoic crinoids along first twenty recomputed principal-coordinate axes, based on data culled to yield separations among contemporaneous genera at least as great as the average separation among congeneric species. See Figure 12 for explanation of graphs. Ordovician-Devonian taxa exceeding morphological extremes of the Carboniferous and Permian are still Dendrocrinina (low values on axis 2), Disparida (low values on axis 3 and low values on axis 4), and Diplobatrada (mostly Rhodocrinitacea; high values on axis 6). In addition, many Ordovician-Devonian Glyptocrinina (high values on axis 2) and Flexibilia (low values on axis 11) exceed Carboniferous and Permian extremes. Carboniferous and Permian taxa exceeding Ordovician-Devonian extremes are still Codiocrinina (high values on axes 3 and 5) and Hexacrinitacea (low values on axis 6). However, very few of the 135 remaining species of Carboniferous and Permian Poteriocrinina lie beyond the range of Ordovician-Devonian data (three species with low values on axis 1, two with high values on axis 2, three with low values on axis 6, and a scattering of species along the higher axes).

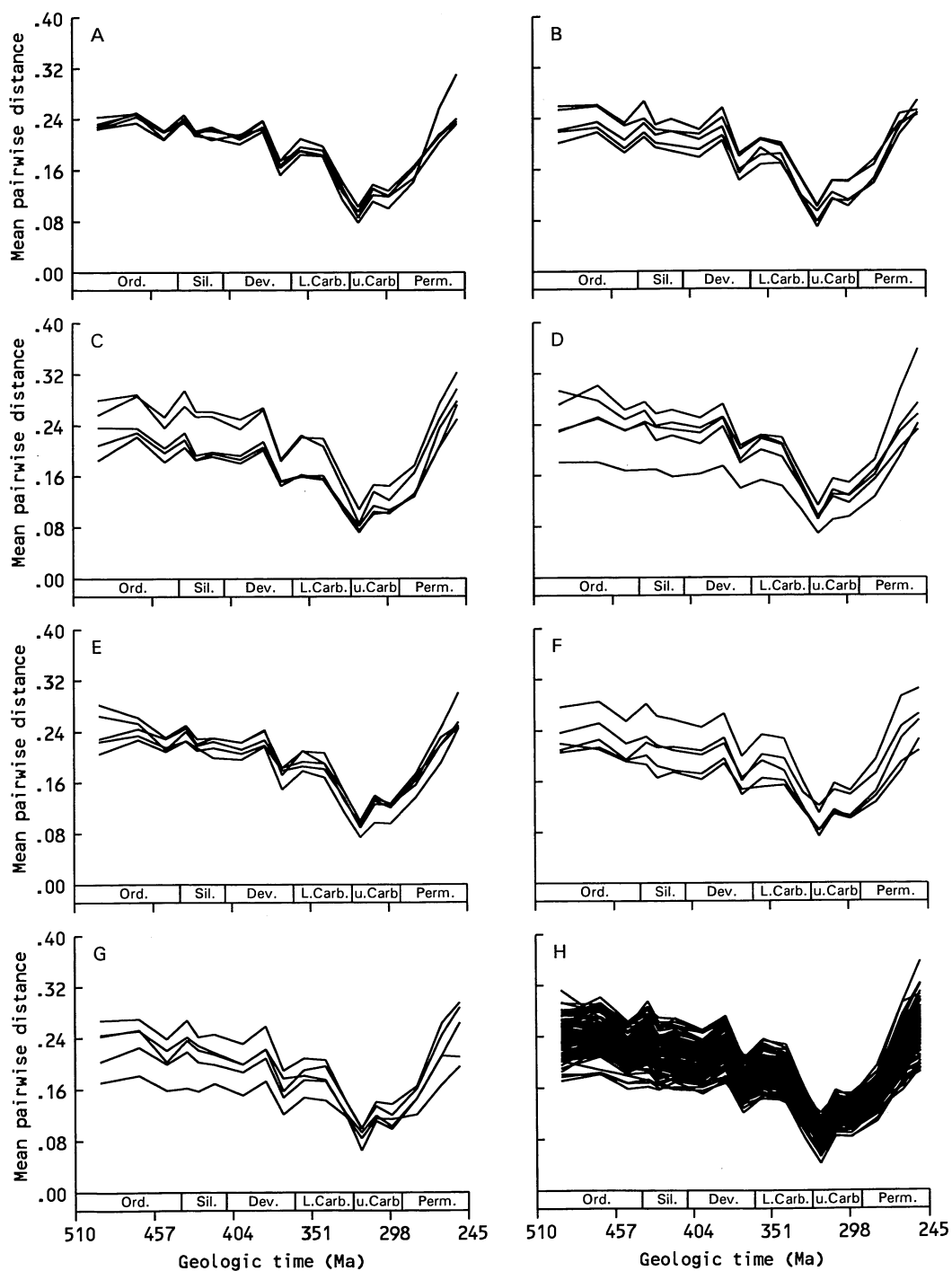


FIG. 16—Time series of morphological disparity with randomly assigned character weights. For each time series, each character is assigned a weight uniform on (0,2). This yields an average weight of unity over a large number of time series. Panels A-G each show only five different time series, so that each trajectory can be followed clearly. Panel H shows 100 time series. Although curves vary

Webster and Lane, 1967; Moore and Strimple, 1969; Broadhead, 1985, 1988a; Simms, 1990; Kammer and Ausich, 1992), changes in diversity within higher taxa corresponded with the evacuation and colonization of whole regions in morphological space. An attempt to explore the effects of differential sampling of crinoid forms suggests that the apparent expansion of poteriocrine cladids into new morphological space is exaggerated by the density with which poteriocrines are sampled.

On the whole, the observed changes in the morphological distribution of crinoids seem small compared with the expectation of evolutionary models of unbounded diffusion (Stanley, 1973; Raup and Gould, 1974; Fisher, 1986; Gould, 1988; McKinney, 1990; Carlson, 1992; Foote, 1993; McShea, 1993a; Valentine et al., 1994), which would predict a rather steady increase in morphological dispersion. Not all morphological extremes reached before the Carboniferous represent absolute limits (Figs. 4, 12). Nevertheless, the importance of functional and structural constraints (Ausich, 1988; Broadhead, 1988b; Kendrick, 1992, 1993) in the large-scale evolution of crinoids is suggested by the small extent to which morphological extremes were exceeded after the Devonian (Figs. 12, 14; see Foote 1995). Although the Lower Carboniferous is often regarded as the acme of crinoids (Wachsmuth and Springer, 1897: p. 163; Springer, 1920: p. 97; Lane and Sevastopulo, 1990), this view reflects their abundance and diversity much more than their variety of form.

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in height, most show the same shape, suggesting that the pattern documented in Figure 1 is not an artifact of an arbitrary weighting scheme. Note that the occurrence of maximal disparity in Ordovician-2 is not completely robust to variation in character weighting. In this and the following figure, high values in Lower Ordovician and Permian-3 may be unreliable because of very small sample size.

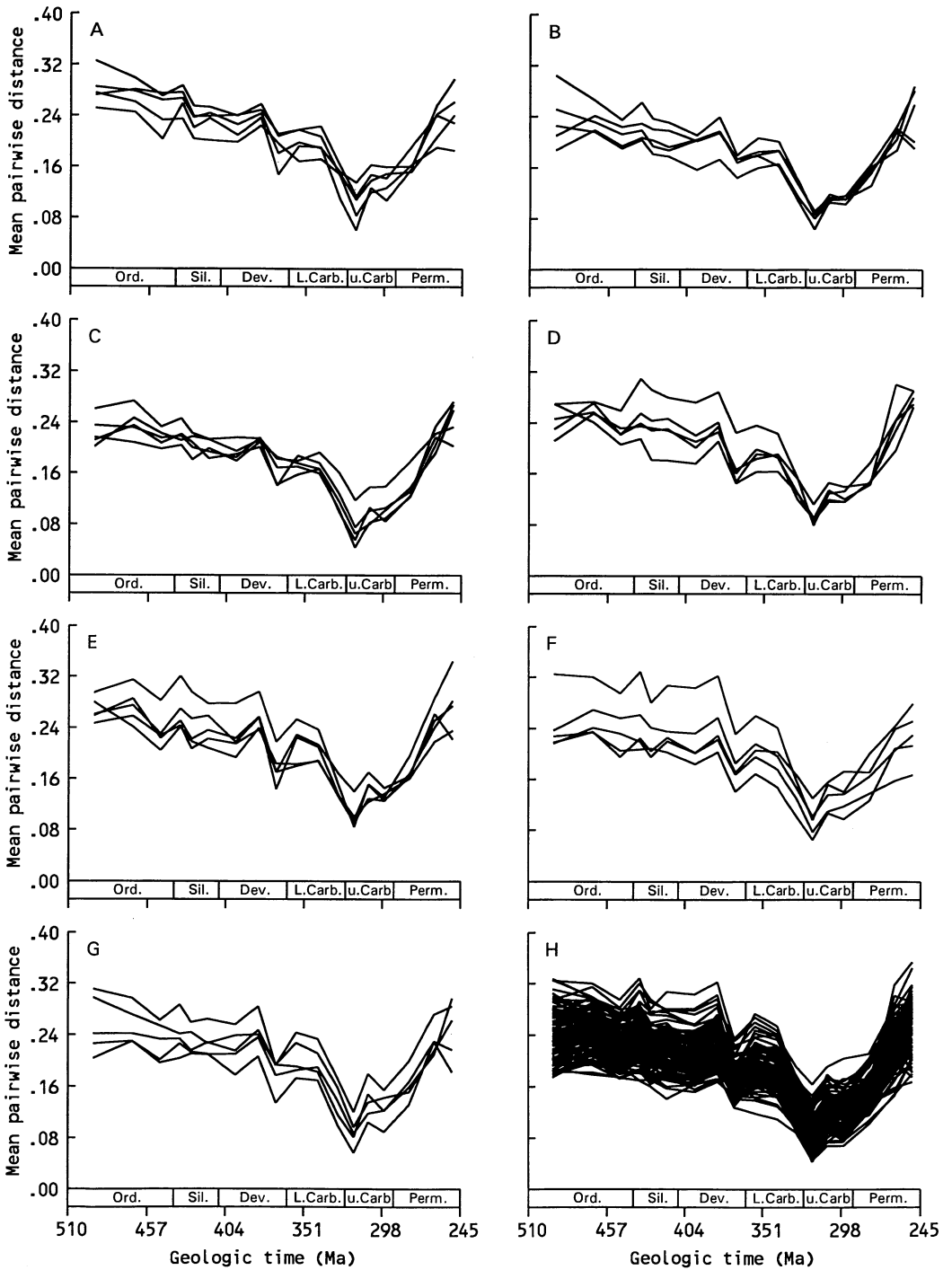


FIG. 17—Time series of morphological disparity based on bootstrap resampling of characters (with replacement). This yields greater variation in character weights while still giving a mean weight of

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unity over many time series. Despite greater variation among the curves, it is still difficult to make a case for a steady increase in disparity over the Paleozoic. However, certain smaller scale features, such as the occurrence of maximal disparity in Ordovician-2, are sensitive to variation in character weighting.

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## APPENDIX 1

## Character Data for Carboniferous and Permian Crinoid Species Used in this Study

Character data for crinoid species used in this study are tabulated on the following pages. Also given are pre-Carboniferous species not included in Foote (1994a), and emendations for species included in Foote (1994a). Unknown character states are indicated by ?; inapplicable states are indicated by N. See Table 1 and Foote (1994a) for explanations of characters and character states. Sources for data are listed in Appendix 2; where no source is given, see Foote (1994a). Two-letter code preceding each species indicates higher taxonomic affinity: CL, Cladida; DB, Diplobathrida; DI, Disparida; FL, Flexibilia; HY, Hybocrinida; and MO, Monobathrida.



CL Parisangulocrinus. zaeiformis	2010?0?0?0NNN115111000N2500N501311?400000	N 1	5	0020120N00010100	N NN	N	NN	0NN30010110??	
DI Calycanthocrinus decadactylus	2000?0?0?0NNN??190N0011231NNNN011?401000	N 1	9	00100NN000030100	N NN	N	NN	0NN300??0???	
<u>Middle Devonian</u>									
DB Opsiocrinus	2?1?060010NN??15131000N2500N5011100411000	N 1	10	00100NN1NN00101	4	111	1	0NN300??0???	
DB Rhinidocrinus	2?0?00701??0??15131000N21N135001210501000	N 1	20	021012101NN00101	13	111	1	0NN2000NNN10	
MO Thamocrinus	2?10?000?0NN??15110000N230NNNN111401100	N 1	10	001012111NN00101	4	111	1	0NN2001100?10	
FL Taxocrinus	20000?0?0NN??15121000N2310N5100?1?401000	N 1	5	0010120N0101010	2	110	N	0NN30010?001?	
CL Proctothylacocri. longus	2?10000?0NN??15111000N2500N5013101400000	N 1	5	0010120N00000100	N NN	N	NN	0NN30010110??	
CL Zostocrinus	2?1?0670?0??0??15111000N1500N5003010401010	N 1	5	0?001??0000?100	N NN?	?	NN?	0NN3001??00??	
								31, 63	
<u>Upper Devonian</u>									
MO Lennecrinus	2?100000?1??0?15111000N230NNNN1?1?401110	N 1	10	0010120N1NN10?01	4	111	?	0NN200??0???	
CL Hallocrinus	2?1007?010NN??15111000N2500N50121?1?401000	N 1	5	0010121100100100	N NN1	1	NN1	0NN3001?110??	
<u>Tournaisian</u>									
DB Cribanocrinus	2?000?0?0NN??15131000N2500N5011310501000	N 1	10	0220110N1NN00101	4	111	1	0NN200??0???	
DB Gilbertocrinus	2?1000?0?0NN??15131000N2500N5011010511000	N 1	20	0?20120N1NN00301	4	111	?	0NN?000NNN10	
DB Rhodocrinites	20100?0?0NN0N1511000N2500N5011200501110	N 1	10	0010110N1NN00101	4	111	?	0NN2000NNN10	
MO Abatocrinus	20100?0?0NN0N1511000N230NNNN1100401000	N 1	20	00100NN1NN00101	7	111	?	0NN20011?010	
MO Actinocrinites	2?1000?0?0NN??15110000N230NNNN1112401010	N 1	30	00100NN1NN00101	7	111	?	0NN30011?0110	
MO Agaricocrinus	2?1?00?010NN??15110000N2?NNNN1000411000	N 1	10	00100NN1NN00201	4	111	1	0NN3000NNN11	
MO Arocrinus	20100?0?0NN0N15110000N230NNNN110?401000	N 1	20	00100NN1NN00101	4	111	1	0NN3000NNN10	
MO Aryballocrinus	2?1000?010NN??15110000N230NNNN121?401000	N 1	10	0020120N1NN00101	4	111	1	0NN2000NNN10	
MO Auliskocrinus	2?1?0?0?0NN??15110000N220NNNN1220401000	N 1	5	0010110N00000100	N NN1	1	NN1	0NN20011000??	
MO Batocrinus	2?1?00?0?0??0??15110000N130NNNN1100401000	N 1	22	00100NN1NN00101	6	111	1	0NN2001110110	
MO Cactocrinus	2?1000?0?0NN??15110000N230NNNN110?401010	N 1	20	00100NN1NN00101	5	111	1	0NN3001110110	
MO Cusacrinus	2?1000?0?0NN0N15110000N230NNNN1110401010	N 1	30	00100NN1NN00101	5	111	1	0NN30011?0110	
MO Cytidocrinus	2?1000?0?0NN??15110000N230NNNN111?401010	N 1	10	022012101NN00101	3	111	1	0NN3001110110	
MO Dialutocrinus	201000?0?0NN??15110000N230NNNN1?00401010	N 1	20	021010111NN00101	4	111	1	0NN2001110110	
MO Dichocrinus	2?1000?0?0NN??15110000N220NNNN1110400010	N 1	5	02010000000100	N NN1	1	NN1	0NN3000NNN10	
MO Displodocrinus	2?100060?0NN??15110000N230NNNN1002401000	N 1	5	02012111NN00201	1	111	?	0NN3001?0111	
MO Dorycrinus	2?1000?0?0NN??15110000N230NNNN1100401000	N 1	24	00100NN1NN00101	4	111	1	0NN3000NNN10	
MO Eretmocrinus	2?1000?0?0NN??15110000N230NNNN1600401000	N 1	20	00100NN1NN00201	6	111	1	0NN30011?0110	
MO Eucladocrinus	2?0001020NN??150N000N21NNNN0210501000	N 1	5	001012101NN00200	N NN1	1	NN1	0NN3000NNN10	
MO Eutrochocrinus	2?1000?0?0NN??15110000N130NNNN1600401000	N 1	40	00100NN1NN00101	7	111	1	0NN2001110110	
MO Macrocristus	2?100060?0NN??15110000N130NNNN111?401000	N 1	18	00100NN1NN00101	4	111	1	0NN3001110110	
MO Megistocrinus	2?1?07?0??0??15110000N230NNNN12?0401000	N 1	20	0010120N1NN00101	9	111	1	0NN?000NNN10	
MO Paradichocrinus	2?1000?0?0NN??15110000N220NNNN1110401010	N 1	5	0020120N1NN00100	N NN1	1	NN1	0NN300?0???	
MO Phyetocrinus	201000?0?0NN0N15110000N230NNNN1100401010	N 1	50	00100NN1NN00101	7	111	1	0NN?000NNN10	
MO Platycrinites	2?1000?0?0NN??150N000N231NNNN0211501000	N 1	5	020121?1NN00100	N NN1	1	NN1	0NN2001000?10	
MO Plemocrinus	2?0001?0?0NN??150N000N21NNNN0201501000	N 1	5	02012101NN00200	N NN?	?	NN?	0NN2000NNN10	
MO Protacocrinus	2??0??0??0??0??15110000N220NNNN1210401001	1	1	5	020100N1NN00100	N NN1	1	0NN200??0???	
MO Steganocrinus	2??0??0??0??0??15110000N230NNNN1102401010	1	1	10	02012101NN00201	3	111	1	0NN?0011?0???
MO Strophlecrinus	201000?0?0NN115110000N220NNNN1211401000	N 1	5	020100N1NN00100	N NN1	1	NN1	0NN2001000110	
MO Strotocrinus	2?1000?0?0NN??15110000N230NNNN1600401110	N 1	20	0?100NN1NN00101	12	111	1	0NN?000NNN10	
MO Sunwaptacrinus	2?1?1?0?0?0??0??15110000N230NNNN1202401010	N 1	20	0010110N1NN00101	5	111	1	0NN2001110110	





MO Aorocrinus	7, 85	2?1?2?000?2?2?15110000N2?N000N1200401000	N 1 12	001000NN1NN00101	5 11?	? ONN300???????
MO Batoocrinus	82, 142	2?100060?0NN??15110000N130NNNN1107401000	N 1 18	001000NN1NN00101	5 111	? ONN2001110110
MO Camptocrinus	104, 142	2?10100?0?0NN??15110000N20NNNN121?401000	N 1 5	0010100N0010100	N NN1	? ONN200???????
MO Dichocrinus	13	201000?0?0NN??15110000N20NNNN121?401000	N 1 5	0010100N00000100	N NN1	1 ONN2000NNNN???
MO Dizyocrinus	8, 140	2?10000?0?0NN??15110000N230NNNN1107401100	N 1 16	0000100N1NN00101	6 111	1 ONN2001110?10
MO Dorycrinus	mississippien.142	2?0000?0?0NN??15110000N130NNNN1112401000	N 1 40	001000NN1NN00101	4 111	1 ONN?000NNNN10
MO Hyrtanocrinus	13, 14	2?10?0?0?0NN??15110000N20NNNN111401000	N 1 20	001000NN1NN00201	6 111	1 ONN?000NNNN10
MO Macrocrinus	138, 142	2?1000?0?0NN??15110000N130NNNN111?401000	N 1 20	001000NN1NN00101	6 111	1 ONN2001110110
MO Paradichoocrinus	polydactylus	2?1000?0?0NN??15110000N20NNNN1112401000	N 1 5	002012121NN00100	N NN1	1 ONN30010001010
MO Platyacrinites	georgii	2?1000?0?0NN??150N1000N231NNNN122?401010	N 1 10	101011101NN00101	3 111	1 ONN200???????
MO Springeracrocrin.	intermedius	200000?0?0NN??15110000N20NNNN121?401001	3 1	5 0020110N1NN10100	N NN1	1 ONN2000NNNN???
MO Strimpelecrinus	coxanus	2?1000?0?0NN??15110000N20NNNN122?401010	N 1 5	0?10100N1NN00100	N NN1	1 ONN200???????
MO Uperocrinus	spiciferus	2?0000?0?0NN??15110000N130NNNN1107401000	N 1 20	001000NN1NN00101	5 111	1 ONN100111????
FL Amphicrinus	101, 169	2?0?0?0?0?0NN??15121010N2?0N5101210501000	N 1 20	00001?0N00000101	7 110	N ONN100???????
FL Artichthyocrinus	springeri	2?00?0?0?0NN??150N1000N2310N5000200501000	N 1 10	00001?0N00000101	3 110	N ONN200???????
FL Caldenocrinus	curtus	2?000?0?0NN??15121000N2?0N5100200501000	N 1 20	00001?0N00000101	6 110	N ONN100???????
FL Enascocrinus	redsdalensis	2?00?0?0?0NN??15121000N2310N5101210401000	N 1 20	000121100000101	3 110	N ONN20010?00??
FL Forbesiocrinus	multibrachiat.101	200000?010NN??15121000N2310N5102210401000	N 1 20	0010121101000101	9 110	N ONN100???????
FL Gaultocrinus	trautscholdi	2?1?0?0?2?2?2?150N1000N210N5010200501000	N 1 5	0?00100N00000100	N NNO	N ONN000???????
FL Mespilocrinus	pringlei	2?0100?0?0NN??15121000N2310N5100200401000	N 1 5	00001?0N00010100	N NNO	N ONN10???????
FL Onychoocrinus	ulrichi	200000?010NN??15121000N2310N5100200401000	N 1 5	0020121000000101	3 110	N ONN2001000010
FL Parichthyocrinus	subovatus	2?0000?0?0NN??15121000N2310N5100200401000	N 1 20	000000N000000101	9 110	N ONN10010?00??
FL Taxocrinus	ungula	2?0000?0?0NN??15121000N23?0N5110107401000	N 1 5	0010100N00110100	5 110	N ONN100100001?
CL Abrotocrinus	unicus	2?1006?0?010NN??15111000N2?0N501320?401000	N 1 5	0210120N00100100	N NN1	1 ONN3001110?2?
CL Adinocrinus	nodosus	2???0?2?1????15111000N250135103001411000	N 1 5	0200120N00100100	N NN?	? ONN300???????
CL Aenigmocrinus	anomalous	2?1?0?0?2?2?2?15111000N2?0N5102200411000	N 1 5	0210100N00120100	N NN1	1 ONN3001?100??
CL Agassizocrinus	lobatus	ONNNNNNNNNNN1511000N110N05202331040N000	N 1 5	0210100N00000100	N NN1	1 ONN200???????
CL Ampelocrinus	mundus	2???0?0?2?2?2?1511000N2500N50111?401000	N 1 5	0010100N00110100	N NN1	1 ONN3001?100??
CL Anartiocrinus	maxvillensis	2?1?0060?2?2?2?15111000N2500N5013110401000	N 1 5	0200100N00000100	N NN1	1 ONN?00???????
CL Anemetocrinus	biseriatis	2?1000?010NN??1511000N2500N5003101401000	N 1 5	0?00NNN1NN00100	N NN1	1 ONN300???????
CL Aphelecrinus	dunlopi	201000?0?0NN??1511000N2500N501311?401000	N 1 5	0000120N00010100	N NN1	? ONN3001?2?0??
CL Aulocrinus	bellus	2?10060010NN??15111000N2?0N501320?411010	N 1 5	0010100N00110100	N NN1	1 ONN3001100???
CL Baryocrinus	asteriscus	2???0?2?1????15111000N2500N5012202401000	N 1 5	0010121000010100	N NNO	N ONN300???????
CL Carlopsocrinus	bullatus	2?1000?0?0NN??15121000N21N135000102501000	N 1 5	0?00????????1000	N NN?	? ONN?0?0???????
CL Cestocrinus	striatus	2?10?0?0?0NN??15121000N1500N5011211?400000	N 1 5	0?20????00010100	N NN?	? ONN?001???????
CL Corythocrinus	fragilis	2?10?0?0?0NN??15111000N1500N502111?401000	N 1 5	0000120N00100100	N NN1	1 ONN2001?00??
CL Cosmetocrinus	gracilis	2?0000?0?0NN??15111000N2500N501511?401000	N 1 5	00101020N00110100	N NN1	1 ONN3001?200??
CL Cryptocrinus	rotundus	2???0?0?1????15111000N250N5023200411000	N 1 5	0?00120N00001000	N NN1	1 ONN?00???????
CL Cyathocrinities	multibrachiat.74, 138, 140	2?1000?0?0NN??15111000N2500N501121?401000	N 1 5	0020120N00010100	N NNO	N ONN200100?010
CL Cydrocrinus	concinus	2?1000?0?0NN??15111000N2?0N5013102401000	N 1 5	0010121100100100	N NN1	1 ONN3001?110???
CL Dymbiocrinus	grandis	2?1?0?0?11????15111000N2500N5001200411000	N 1 5	0010100N00110100	N NN1	1 ONN3001?1????
CL Dinetocrinus	compactus	2?10?0?0?0NN??15111000N2?0N5013200411000	N 1 5	0000110N00110100	N NN1	1 ONN3001?10???
CL Eratocrinus	commaticus	2???0?0?2?2?2?15111000N2500N5012201411000	N 1 5	0?00121100000100	N NN1	2 ONN30011100???
CL Eupachyrcrinus	quatuordecimb.42	2????????????15111000N2?0N5013200411000	N 1 5	02001?1?NN000100	N NN?	? ONN?00???????
CL Fifeocrinus	tielensis	2???0?2?2?2?2?15111000N2500N501311?401000	N 1 5	0010120N00000100	N NN?	? ONN?00???????
CL Forthocrinus	lepidus	2?1000?0?0NN??15111000N2500N5003201411000	N 1 5	0?10100N00120100	N NN1	1 ONN300???????
CL Harmostocrinus	porosus	2?1000?0?0NN??15111000N2?0N5013200411000	N 1 5	0210110N00110100	N NN1	1 ONN3001?110???

CL Histocrius	coreyi	138	2?1000?0?0NN??15111000N2500N501321?401000	N 1	5	0210100N00110100	N NN1	1	ONN3001?110??
CL Hydreionocrius	amplus	169	2?1000?0?0NN??15111000N250135003200401000	N 1	5	000012121NN00100	N NN1	1	ONN3001111???
CL Hydlocetrius	brtareus	37, 82	2?1006?0?0????15111000N2??0N501320?401010	N 1	5	0010121100000100	N NN1	1	ONN300111???
CL Hypselocrius	hoveyi	36, 138	2?0000?0?0NN??15111000N1500N501311?400000	N 1	5	0210100N00000100	N NN1	1	ONN3001?110??
CL Intermediacrius	hinmani	18	2?1?070?0????15111000N2??0N5013200411000	N 1	5	0200110N1NN00100	N NN1	1	ONN3002??2???
CL Lageniocrius	seminulum	46	2??2?0?0????10NNNNNNN310N50N0111501000	N 0	N	NNNNNNNNNNNN00	N NN1	N	ONN30011NNNN00
CL Lanecrius	depressus	37, 138	2?1000?0?0NN??15111000N2??0N501320?401000	N 1	5	0010100N00120100	N NN1	1	ONN3001?120??
CL Lebetocrius	grandis	36, 48	2?1070?010NN??15111000N2500N5?11?0?401000	N 1	5	0000120N00100100	N NN1	1	ONN3001??0??
CL Linocrius	praemorsus	38, 82, 85	2??2?0?0????15111000N2??0N500320?411000	N 1	5	0200121100100100	N NN1	1	ONN300??2???
CL Lophocrius	minutus	35, 99	2010000010NN1115110000N2500N50111?401000	N 1	5	00100NN00100100	N NN1	1	ONN3001?100??
CL Pachylocrius	aequalis	37, 79, 138	2?10000?0?0NN??15111000N2??0N501320?401000	N 1	5	0000120N00100100	N NN1	1	ONN3001??2???
CL Parascytalocrius	validus	37	2?0000?0?0NN??15111000N2??0N501320?4?1000	N 1	5	0200100N00000100	N NN1	?	ONN3001?100??
CL Parazeacrinites	konincki	169	2??2?0?0????15111000N2500N5003001411000	N 1	5	000121100000100	N NN1	?	ONN300??2???
CL Pariscrocinus	crawfordsvill.	138	2??2?0?0????15111000N2500N501311?401000	N 1	5	0010120N0010100	N NNO	1	ONN3001?110??
CL Pelliscrocinus	hexadactylus	40, 75, 138	2?10000010NN??15111000N2500N501320?401000	N 1	5	00201210000010100	N NNO	1	ONN30010100??
CL Phanocrius	calyx	169	2??2?0?0????15111000N2500N5003200411000	N 1	5	0000100N00000100	N NN1	1	ONN300??2???
CL Sarocrius	nitidus	54	2?1000?0?0NN??15111000N2500N5113200411000	N 1	5	0200010N000010100	N NN1	?	ONN3001?101??
CL Scotiacrius	tyriensis	168, 169	2??2?0?0????15111000N2??0N5013200411000	N 1	5	0200010N000010100	N NN1	?	ONN300??2???
CL Scytalocrius	decadactylus	36, 78	2?00?0?0?0NN??15111000N2500N5013200411000	N 1	5	0010100N000000100	N NN1	1	ONN300??2???
CL Springericrius	magniventrus	67, 100	2?1000?0?0NN??15111000N2500N501311?401010	N 1	5	0010100N000000100	N NN1	1	ONN3001111010
CL Staphylocrius	bulgeri	17, 20	ONNNNNNNNN15111000N210N501311?401000	N 1	5	0010120N00000100	N NN?	?	ONN3001?1?00??
CL Ulrichicrius	agnatus	36	2?0000?0?0NN??15111000N2500N501311?401000	N 1	5	0200110N000010100	N NN1	1	ONN300??2???
CL Ureocrius	bockschii	169	2?10?0?0?0NN??15111000N2500N501311?401000	N 1	5	0000NNN00110100	N NN1	1	ONN3001??2???
CL Woodocrius	liddesdalensi.	169	201000?010NNON15111000N2500N500310401000	N 1	5	000010N000000100	N NN1	1	ONN3001??2???
CL Zeacrinites	magnoliaeform.	20, 88, 104	2??2?0?0????15111000N2500N500310401000	N 1	5	000010N000000100	N NN1	1	ONN3001??2???
DI Allagacrius	austini	23, 169	2??2?0?0????15111000N250115003201411000	N 1	5	000012100000100	N NN?	?	ONN3001??2???
DI Allocatillocrius	carpenteri	102	2?0000?0?0NN??150N0010N231NNNNN1100100000	N 1	12	2?00??2?00030100	N NN?	?	ONN300??2?00
DI Eucatillocrius	bradleyi	102, 138	200000?0?0NNON150N0010N231NNNNN0110100000	N 1	24	20000NNN00030100	N NNO	N	ONN30010100??
DI Halystocrius	nodosus	87, 103	2?70000?0?0NN??140N00112231NNNNN001?1010000	N 1	3	02001213000020100	N NNO	N	ONN20010100??
Serpukhovian									
MO Acrocrius	shumardi	24, 91, 142	2?1000?010NN??15111000N220NNNNN1220401001	20	1	1010100N1NN00201	5 ON1	1	ONN2000NNNN10
MO Camptocrius	cirriifer	20, 104	2?1100?0?0NN??15111000N220NNNNN121?401000	N 1	5	0010100N00100100	N NN1	1	ONN200??2???
MO Pterotocrius	acutus	24	2??2?0?0????15111000N220NNNNN1102401000	N 1	3	00100NN1NN00100	3 ON1	1	ONN2000NNN11
FL Cibolocrius	africanus	134	2??2?0?010NN??15111000N2?10N5011200401000	N 1	5	0000100N00000100	N NNO	N	ONN200??2???
FL Onychocrius	pulaskiensis	101	200000?010NN??15111000N2310N5010120?401000	N 1	5	0010121000000101	1 110	N	ONN30010?20??
FL Taxocrius	whitfieldi	24, 101	2?0000?0?0NN??15111000N2310N500200401000	N 1	20	00101100N0010101	5 110	N	ONN10010?0010
CL Altimocrius	ornatus	20, 109	2??2?0?0????15111000N2500N5003200411000	N 1	5	0000121100000100	N NN1	1	ONN3001?1?2??
CL Ampelocrius	kaskaskiensis	52, 124	201000?0?111??15111000N2500N50120?401000	N 1	5	0010110N00110100	N NN1	1	ONN300??2???
CL Anartiocrius	lyoni	45, 104	2??2?0?0????15111000N2500N5013110401000	N 1	5	0200100N00000100	N NN1	1	ONN300??2???
CL Bronaughicrius	randolphensis	20, 56	2?1?0?0?0????15111000N2500N5013102401000	N 1	5	0000100N00110100	N NN1	?	ONN300??2???
CL Culmicrius	figuratus	19, 64, 110	2?1000?0?0NN??15111000N2500N501311?401000	N 1	5	02101?0N00110100	N NN1	1	ONN3001?100??
CL Cymbiocrius	grandis	24, 104	20100060?1??15111000N2?0N5012300411000	N 1	5	0010100N00110100	N NN1	1	ONN300??2???
CL Eupachycrinus	boydii	24, 57	2?1?0?0?0????15111000N2??0N5013200411000	N 1	5	0200110N1NN00100	N NN1	1	ONN300??2???
CL Heliosocrius	aftonensis	42, 80	2?1?0?0?0????15111000N25?0N5013201411010	N 1	5	0?0120N00110100	N NN1	?	ONN3001?1???
CL Hydreionocrius	goniodactylus	110, 123	2?1000?0?0NN??15111000N2??135500320?401000	N 1	5	000012121NN00100	N NN1	?	ONN3001111???

CL Patanocrinus	110, 116	2????000??????15111000N2500N5003101401000	N 1	5	0000120N00000100	N NN1	? ONN300111????
CL Paracymbiocrinus	19	2????6?0?00??????15111000N2500N5001200411000	N 1	5	0010100N00020100	N NN1	2 ONN300????????
CL Pelecocrinus	70	2????70????????15111000N2500N500370?401000	N 1	5	0010120N00000100	N NN1	1 ONN?00????????
CL Pentaramicrinus	42, 158	2????0?0??????15111000N2500N5013200411000	N 1	5	00000NN00000100	N NN1	1 ONN3001?200??
CL Phacelocrinus	20, 24	2?1006?010NN??15111000N2500N5013110401000	N 1	5	0010100N00110100	N NN1	? ONN3001?100??
CL Phanocrinus	24, 42	2?100070?0NN??15111000N2500N5013200411000	N 1	5	0000100N00000100	N NN1	? ONN3001?11????
CL Putaskicrinus	24, 34	2?1?0070??????15111000N2500N501310?401000	N 1	5	0010120N00100100	N NN1	1 ONN2001?10???
CL Rhopocrinus	24, 53	20100070?0NN??15111000N2?0N501370?401000	N 1	5	0?10121100100100	N NN1	? ONN3001?100??
CL Scammatocrinus	20	2????????????15111000N2500N5013200401000	N 1	5	0?101?0N00110100	N NN1	1 ONN3001?1????
CL Scytalocrinus	112	2????0?1??????15111000N2500N5003100401000	N 1	5	0010100N00000100	N NN1	1 ONN300????????
CL Telikococrinus	20, 111	2?1?0701?0????15111000N2500N5013200401000	N 1	5	000012101NN00100	N NN1	1 ONN3001?1????
CL Tholocrinus	34, 44, 104, 159	2?1?06?0??????15111000N2500N5003000411000	N 1	5	020012111NN00100	N NN1	? ONN30011101??
CL Ultrichocrinus	109	2?1?00?0??????15111000N2500N501311?401000	N 1	5	0200110N00000100	N NN1	1 ONN300????????
CL Woodocrinus	104, 169	201000?0?0NN??15111000N2500N501310?400000	N 1	5	0000110N00000100	N NN1	1 ONN3001?200??
CL Zeacrinites	34, 88, 104	2???00?0??????15111000N2500N5003201411000	N 1	5	0000121100000100	N NN1	2 ONN30011100??
<b>Bashkirian</b>							
CL Aglaocrinus	89, 106, 128	2???0?0?1????15111000N2500N5012300411000	N 1	5	0000120N1NN00100	N NN1	1 ONN300????????
CL Alciocrinus	43, 88, 104, 125	2?1?00?0??????15111000N2500N5003201411000	N 1	5	0000121100000100	N NN1	? ONN300111????
CL Diphuicrinus	89, 92, 130	2????0?0??????15111000N2?0N5011200411000	N 1	5	0000100N00100100	N NN1	? ONN300????????
CL Mathericrinus	92, 118, 151	2????0?01????15111000N2500N5013300401000	N 1	5	0000100N1NN00100	N NN?	? ONN200????????
CL Morrowcrinus	92, 150	2????0?0?0NN??15111000N2500N5013110401000	N 1	5	0000100N00000100	N NN1	? ONN300????????
CL Oxyocrinus	135	2????00?0?0NN??15111000N25?2?5?1320?401000	N 1	5	0?10120N00020100	N NN1	1 ONN300????????
CL Paragassizocrinus	tarri	0NNNNNNNNNN15111000N210N501121040N000	N 1	5	0000100N00000100	N NN1	? ONN?00????????
CL Proallosocrinus	92	2???0?0?0????15111000N2500N5011200411000	N 1	5	0?10100N00000100	N NN1	1 ONN300????????
CL Scytalocrinus	crassibrachia.92	2?1?0000??????15111000N2500N501320?401000	N 1	5	0000100N000000100	N NN1	? ONN300????????
<b>Moscovian</b>							
FL Cibolocrinus	90	2????0?0??????15111000N2310N5011200401000	N 1	5	0?00110N000000100	N NNO	N ONN000????????
FL Synerocrinus	101	2?00007010NN??15121000N2310N5101210401000	N 1	20	0010121100000101	5 110	N ONN20010?0010
CL Aglaocrinus	151	2?1?00701????15111000N2500N5012200411000	N 1	5	0200100N1NN00100	N NN?	? ONN300????????
CL Anchicrinus	135	2???00?1????15111000N2500N5003200411000	N 1	5	0000121100000100	N NN?	? ONN300111????
CL Anobascrinus	116	2???00?1????15111000N2500N5013100401000	N 1	5	0?10120N00010100	N NN1	1 ONN3001111????
CL Araeocrinus	135	201006010NN??15111000N1500N501111?401000	N 1	5	0?10110N00101000	N NN1	1 ONN30010110??
CL Cricocrinus	29, 109, 135	2???0?0?2????150N1000N2500N5000300501000	N 1	5	0?00100N1NN00100	N NN1	? ONN300????????
CL Cromyocrinus	170	2?10007010NN??15111000N2500N5013300401000	N 1	5	0?000NN00000100	N NN1	1 ONN30010000??
CL Dicromyocrinus	170	2?10007010NN??15111000N2?0N5013000401000	N 1	5	0000100N00100100	N NN?	? ONN300????????
CL Eimocrinus	135	????????????15111000N2?0N500300?41?000	N 1	5	0000121100000100	N NN1	1 ONN300111????
CL Grafhamicrinus	116	2?10000010NN??15111000N2500N5011200411000	N 1	5	0000100N1NN10100	N NN1	1 ONN300????????
CL Hydroicrinus	135	2???0600??????15111000N2500N501311?401000	N 1	5	00101?0N00120100	N NN1	? ONN?001?????0??
CL Lecobascrinus	135	2?10?0?0?0NN??15111000N25?135?0120?411000	N 1	5	0?00100N00000100	N NN1	? ONN300????????
CL Metacromyocrinus	holdenvi llens.11, 116	2?1?00701????15111000N2500N5012200401000	N 1	5	0000100N1NN00100	N NN1,	1 ONN200????????
CL Metaphrimestocri .spiniiferus	11, 95, 116	201006010NN??15111000N2500N5013100401000	N 1	5	0000120N00000100	N NN?	? ONN300111????
CL Miatschkovocrinus	3, 170	2?1?00001????15111000N2500N5013202411000	N 1	5	0010110N00110100	N NN1	1 ONN3001?1?0??
CL Mooreocrinus	170	2?1000?0?0NN??15111000N2500N5013200401000	N 1	5	0000100N00000100	N NN1	? ONN300????????
CL Moscovicrinus	170	2?1000?0?0NN??15111000N2500N5013110401000	N 1	5	0?10120N00000100	N NN1	1 ONN300????????
CL Neoprotencrinus	brachiatius	2???0?0?0????150N1000N2500N5000200511000	N 1	5	0000100N1NN00100	N NN?	? ONN300????????

CL Neozaeacrinus	90, 117	2??2??0101????151111000N2500N5013200401000	N 1	5	0000120N00010100	N	NN1	4	0NN3001???????
CL Parethelocrinus	116	2?10007010NN??151111000N2500N501220041000	N 1	5	0200110N1NN00100	N	NN1	1	0NN3002???????
CL Pegocrinus	49, 170	2010007010NN??151111000N2500N5013102401000	N 1	5	0010100N0000100	N	NN1	1	0NN3002???????
CL Pirasocrinus	90, 135	2????0????????151111000N2500N5003001411000	N 1	5	0000120N00000100	N	NN1	2	0NN300111?????
CL Plaxocrinus	116	2?1?00701????151111000N2500N5003200411000	N 1	5	0?00121100100100	N	NN?	1	0NN30011110????
CL Schedexocrinus	11, 116	2????0????????151111000N2500N500320141000	N 1	5	0000120N000020100	N	NN1	2	0NN300111?????
CL Schistocrinus	90	2????0????????151111000N2500N5003000411000	N 1	5	0?00120N00020100	N	NN?	2	0NN300111?????
CL Sciadiocrinus	90, 125	2?1000?0?0NN??151111000N2500N50013110401000	N 1	5	0001000N00110100	N	NN1	1	0NN3002???????
CL Scytalocrinus	89, 90, 92, 135	2????0????????151111000N2500N5003200411000	N 1	5	0010120N1NN00100	N	NN1	1	0NN3002???????
CL Sellardsicrinus	90, 135	2?1?00001????151111000N2500N5003200411000	N 1	5	0?10120N1NN00200	N	NN1	1	0NN3002???????
CL Stellarocrinus	116	2?1?00001????151111000N2500N5013?0?4?2?010	N 1	5	0200110N00110100	N	NN1	1	0NN3002???????
CL Tarachocrinus	116, 151	2?1?00701????151111000N2500N5013200411000	N 1	5	0?10120N00000100	N	NN1	2	0NN3002???????
CL Texacrinus	116	2?1?00701????151111000N2500N5013100411000	N 1	5	0?10120N00000100	N	NN1	2	0NN3002???????
CL Ullocrinus	116	2????0????????151111000N2500N502221?401000	N 1	5	0?101???1NN10100	N	NN?	2	0NN?002???????

Stephanian									
MO Caucacrocrinus	91	2010007010NN??151111000N220NNNN1310401001	5 1	5	0?20100N00110100	N	NN1	1	0NN?000NNNN10
FL Cibolocrinus	96	2???200??1????151111000N2?10N5001200401000	N 1	5	0000100N00000100	N	NNO	N	0NN1002???????
CL Aeglaocrinus	95, 120	2????0????????151111000N2500N5012200411000	N 1	5	0200110N1NN00100	N	NN1	1	0NN3002???????
CL Aesticrinus	65, 82, 132	2?1006?01????151111000N2500N501201401000	N 1	5	0?10100N00100100	N	NN1	1	0NN30011110????
CL Alltosocrinus	95, 108, 133	2?1006?01????151111000N2500N501200411000	N 1	5	0?100NN00110100	N	NN1	1	0NN3002???????
CL Apographiocrinus	90, 133	210000010NN??151111000N2500N501200411000	N 1	5	0010100N0010100	N	NN1	1	0NN3002???????
CL Brabeocrinus	133	201000?010NN??151111000N2??0N5003201411010	N 1	5	0010110N00110100	N	NN1	1	0NN3001?100???
CL Chlidocrinus	132	2?1000?0????151111000N2??0N501120?401010	N 1	5	0010120N00110100	N	NN1	2	0NN3001?101???
CL Clathrocrinus	133	2010000010NN??151111000N2310N5003200411000	N 1	5	0020121000030100	N	NNO	N	0NN30010100???
CL Contocrinus	133	2110000010NN??151111000N2??0N5001200411000	N 1	5	0000100N00110100	N	NN1	1	0NN3002???????
CL Delocrinus	94, 95	2???200??1????151111000N2500N5011200411000	N 1	5	0000120N1NN10100	N	NN1	2	0NN3002???????
CL Elibatocrinus	133	2?0000?0?0NN??151111000N1310N501311?401000	N 1	5	0010100N00110100	N	NN1	1	0NN?20011100???
CL Erisocrinus	90, 133	2010000010NN??150N1000N2500N500201501000	N 1	5	0000100N1NN00100	N	NN1	1	0NN3001?100???
CL Exocrinus	108, 133	2010000010NN??151111000N2500N5003101411000	N 1	5	0010120N00020100	N	NN1	3	0NN3001?100???
CL Exoriocrinus	133, 167	2?1006?0?0NN??151111000N2500N501321?401000	N 1	5	0010110N00110100	N	NN1	1	0NN3002???????
CL Grafhamicrinus	107	2?1?00001????151111000N2500N5011200411000	N 1	5	0010120N00000100	N	NN?	2	0NN3002???????
CL Haeretocrinus	93, 133	201000?0110??151111000N2500N50131?0?401000	N 1	5	0000100N1NN00100	N	NN1	1	0NN3001?1?????
CL Halogetocrinus	97, 121	2?1?00001????151111000N2500N500120?401000	N 1	5	00101130000100	N	NN1	1	0NN3001?100???
CL Hydroicrinus	83, 95, 133	2?1?000?0????151111000N2500N500120?401000	N 1	5	001011200000100	N	NN1	1	0NN3001?1?????
CL Laudonocrinus	90	2?1?000?0????151111000N2500N5001311?401000	N 1	5	0000100N1NN00100	N	NN1	2	0NN3002???????
CL Microcaracrinus	133	2?1?00001????151111000N2?0N5001201411000	N 1	5	0000100N1NN00100	N	NN1	2	0NN3002???????
CL Parulocrinus	133	2?1?00001????151111000N2500N5013200401000	N 1	5	0210110N1NN00100	N	NN1	1	0NN3002???????
CL Plaxocrinus	86	2????0????????151111000N2500N5002201411000	N 1	5	0000110N00010100	N	NN?	2	0NN300111?????
CL Plummericrinus	86	2????6?7????151111000N2500N5011200401000	N 1	5	0?001???00000100	N	NN?	2	0NN?002???????
CL Polusocrinus	113	2?1000010NN??151111000N2500N5013?0?401000	N 1	5	0?00120N00000100	N	NN1	1	0NN300111?????
CL Polygonocrinus	133	2?1?006?1????151111000N2500N50?03?01411000	N 1	5	0?00120N1NN00100	N	NN1	2	0NN3002???????
CL Proletocrinus	133	2?100000?0NN??151111000N2500N5001201411010	N 1	5	0?00120N1NN00100	N	NN?	2	0NN3001?100???
CL Stellarocrinus	110, 133	2???0000????151111000N2500N5013100411000	N 1	5	000012100100100	N	NN1	1	0NN30011100???
CL Stenopocrinus	115, 129	2????00?1????151111000N2500N5003001411000	N 1	5	0?00120N00000100	N	NN1	1	0NN?001?1?0???
CL Terpnocrinus	95, 133	2????00?1????151111000N2500N5013200401000	N 1	5	0?00120N00000100	N	NN1	1	0NN?001?1?0???

CL Texacrinus	114, 132	2?1000?010NN??15111000N25?0N5013200411000	N 1	5	0010110N00100100	N NN1	1	0NN300???????
CL Ulocrinus	133	2?0000?011107??15111000N2500N501231?401000	N 1	5	0010100N11NN00100	N NN1	1	0NN?00???????
DI Kallimorphocrinus. lasallensis	133	2????0000????150N000N231NNNNN0302400000	N 1	8	12000NNN00030100	N NNO	N	0NN300???????
<b>Permian-1</b>								
MO Neocamptocrinus	164	2?0001?021107??151110000N220NNNN1210401000	N 1	10	0?10?????0?010101	2 11?	?	0NN?00NNNN00
FL Cibolocrinus	21, 22	2????0001????15111000N2310N5001200401000	N 1	5	0000100N00000100	N NNO	N	0NN100???????
FL Nevadaocrinus	68, 155	210000?010NN??15111000N23113510320?401000	N 1	5	0?10120N01010101	1 110	N	0NN?00???????
FL Trampidocrinus	68, 155	210000?010NN??151210?0N231135110?1?401000	N 1	40	0?101?0N01010101	1 110	N	0NN?00???????
CL Artyocrinus	68, 155	2????00?0????15111000N2?0N501321?401000	N 1	5	0200110N00000100	N NN1	1	0NN300???????
CL Brabeocrinus	68, 155	2?10000010NN??15111000N25?0N501120?411010	N 1	5	0010120N00110200	N NN1	1	0NN300?1100??
CL Cetonocrinus	68, 155	2????0????????15111000N2?0N5011?02411000	N 1	5	0?101?0N00110100	N NN1	?	0NN300?1?0??
CL Elibatocrinus	68, 155	2?10000?010NN??15111000N2310N501311?400000	N 1	5	0?101?0N00110100	N NN1	1	0NN300?1?0??
CL Erisocrinus	68, 155	2?10000?0NN??150N1000N2500N5010201511000	N 1	5	0000100N1NN00100	N NN?	?	0NN300???????
CL Exocrinus	68, 155	2?1000?0?0NN??15111000N2500N5001100000000	N 1	5	0010121200010100	N NN1	1	0NN300???????
CL Microcaracrinus	86	2????00?1????15111000N2?0N5013200411000	N 1	5	0?10120N00010100	N NN1	?	0NN300?1110??
CL Moscovocrinus	68	2?10000?010NN??15111000N2500N5011200411000	N 1	5	0000100N00000100	N NN?	?	0NN300???????
CL Nebraskacrinus	86, 94	2????00701????15111000N2500N5013110401000	N 1	5	0?0012100000100	N NN1	1	0NN2001100??
CL Nezeacrinus	68	2????0?0????15111000N250115003200401000	N 1	5	0000121100000100	N NN1	4	0NN300111????
CL Plaxocrinus	68, 155	2????0?0????15111000N25?0N501320?4?1000	N 1	5	0?001211000100100	N NN1	1	0NN300???????
CL Stuartwellerocrinus. corbatoi	68, 155	2?0000?0?0NN??15111000N2?10N501110401000	N 1	5	0000100N00010100	N NN1	1	0NN300???????
CL Synphocrinus	68, 155	2?1000?010NN??15111000N2500N501311?401000	N 1	5	0?10121100010100	N NN1	4	0NN30011100??
CL Tundracrinus	170	201000?0?0NN??15111000N2500N5013?1?401000	N 1	5	0000120N00000100	N NN?	?	0NN3001?00??
DI Kallimorphocrinus. eaglei	119, 155	2?000000?0NN??150N0010N21NNNNN0302401000	N 1	12	22000NNN000020100	N NNO	N	0NN300???????
<b>Permian-2</b>								
MO Dichocrinus?	165	2????00?0?0NN??151110000N220NNNN11?1?401000	N 1	5	0?201????00110100	N NN?	?	0NN?00???????
MO Neocamptocrinus	164	200001?021107??15111000N2310N5001210401000	N 1	10	0?101?2?000?0101	2 11?	?	0NN?00NNNN00
MO Stomiocrinus	153	2????0????????151110000N220NNNN111?401000	N 1	5	0010100N00110100	N NN1	1	0NN?00???????
FL Ancistrocrinus	147	2????0????????150N1100N2?0N5000200511000	N 1	5	0?101?0N00010100	N NNO	N	0NN?00???????
FL Calycocrinus	76, 143	2????0?01????150N1010N210N5110010100000	N 1	5	0200100N00000100	N NNO	N	0NN000???????
FL Loxocrinus	143	2????0?0?1????15110100N2210N5011310401000	N 1	5	0010110N00000100	N NNO	N	0NN010???????
FL Permibrachypus	147	0NNNNNNNNN150N0000N11NNNNN00005NN000	N 1	5	00000NN00000100	N NNO	N	0NN000???????
FL Petrocrinus	144, 147	2????0????????15111000N210N5011111501000	N 1	5	0000100N00000100	N NNO	N	0NN100???????
FL Plagiocrinus	144	2????0????????150N10N21NN1N00100000000	N 1	5	0200110N00000100	N NNO	N	0NN200???????
FL Prophyllocrinus	143, 144	2?0000010NN??150N1000N210N5010310511000	N 1	5	0020110N00000100	N NNO	N	0NN000???????
FL Syntomocrinus	143	2?0?060????????150N100N2310N5001300511000	N 1	5	0000110N00000100	N NNO	N	0NN000???????
CL Abrachiocrinus	145	2????0????????150N1000N2310N5020310501000	N 0	N	NNNNNNNNNNNN000	N NNN	N	0NNNN1NNNNN00
CL Acariatiocrinus	144, 145	2????00?1????10NN1NNNNN310N50N0211501000	N 0	N	NNNNNNNNNNNN000	N NNN	N	0NNNN0NNNN00
CL Anechocrinus	153	2????0?1????15111000N25?0N5013210401000	N 1	5	0?101?0N00010100	N NN?	?	0NN?0?0???????
CL Calcaelispongia	136, 153	2?1006601110?15111000N2500N5021402411000	N 1	5	0?100NN00110100	N NN1	1	0NN?000NNNN?0
CL Clitocrinus	2	2????0????????10NN1NNNN310N51N0111501000	N 0	N	NNNNNNNNNNNN000	N NNN	N	0NNNN1NNNNN00
CL Coenocystis	145	2????0????????10NN1NNNN1N0N50N0101501000	N 0	N	NNNNNNNNNNNN000	N NNN	N	0NNNN1NNNNN00
CL Cosmetocrinus?	154	2?1000?010NN??15111000N1?0N502311?401000	N 1	5	0?10120N00110100	N NN1	?	0NN3001?2?????
CL Dichostreblocrinus. timorensis	2, 76	2????000?0????10NN1NNNN310N50N0212501000	N 0	N	NNNNNNNNNNNN000	N NNN	N	0NNNN1NNNNN00
CL Embryocrinus	143, 145	2????00?1????15131000N0310N5020101501000	N 0	N	NNNNNNNNNNNN000	N NNN	N	0NNNN1NNNNN00

CL Eopliidocrinus	heckeri	2, 3	0NNNNNNNNNN10NN1NNNN1NON50N00105NN000	N 0	N	NNNNNNNNNNNNNN00	N NNN	N	0NNN00NNNN00
CL Gissocrinus?	voiseyi	163	2????070????????15111000N2310N5011?17401010	N 1	5	0?20120N00010100	N NNO	N	0NN?2001?2?0???
CL Graphiocrinus	pumilus	143, 149	2????070????????15111000N250N5011200411000	N 1	5	00001?0N00020100	N NN?	N	0NN30011?00???
CL Hemistreptacron	abrachiatum	2	2????070????????10NN1NNNN310N50N0210501000	N 0	N	NNNNNNNNNNNNNN00	N NNN	N	0NNNN1NNNN00
CL Jimbacinus	bostocki	137	2?1000?070NN??15111000N250N5021312411000	N 1	5	00100NN00110100	N NN1	N	0NN30010000???
CL Lageniocrinus	maximus	2	2????070????????10NN1NNNN310N50N0101501000	N 0	N	NNNNNNNNNNNNNN00	N NNN	N	0NNN00NNNN00
CL Neolageniocrinus	shichanensis	2	2????070????????10NN1NNNN310N50N0101501000	N 0	N	NNNNNNNNNNNNNN00	N NNN	N	0NNN00NNNN00
CL Neozacrinus	peramplius	148	2????070????????15111000N250N5011??7401010	N 1	5	0?10121000010100	N NNO	N	0NN300100?0???
CL Nowracrinus	ornatus	163	2?1700001????15111000N210N501111401000	N 1	5	0?01?1?1?????00	N NN?	N	0NN?00?7?????
CL Occiducrinus	australis	153	2????006?1????15111000N2500N5011?1301401000	N 1	5	0?00?2?00000100	N NN?	N	0NN?00?7?????
CL Paragraptiocrinus	exornatus	143, 144, 148	2????00001????150N1000N2500N5010201511000	N 1	5	00001?0N00000100	N NN?	N	0NN300?7?????
CL Parastachyocrinus	malaitanus	144, 149	2????070????????150N1000N2500N5001200411000	N 1	5	00001??00020100	N NN?	N	0NN300?101???
CL Permilocrinus	immatulus	149	2????070????????15111000N250N5013200411000	N 1	5	00001??00020100	N NN?	N	0NN300?101???
CL Prolobocrinus	permicus	148	2????0701????15111000N210N5000202511000	N 1	5	00101?0N00110100	N NN1	N	0NN300?7?????
CL Skaiocrinus	granulosus	153	2????0701????15111000N250N5011001411000	N 1	5	00001??00000100	N NN?	N	0NN300?7?????
CL Spheniscocrinus	australis	154	????????????15111000N250N50113?0?40?000	N 1	5	00101?0N00110100	N NN1	N	0NN300?7?????
CL Tapinocrinus	timoricus	143, 149	2????0070????15111000N250N501001001411000	N 1	5	00001??00000100	N NN?	N	0NN300?1?1???
CL Tenagocrinus	sulcatus	145	2????070????15131000N110N5020300501000	N 1	5	0?200NN0010100	N NNO	N	0NN001NNNN00
CL Timorechinus	mirabilis	143	2????000?1????15121000N210N5100201401000	N 1	5	0110121000030100	N NNO	N	0NN3001110101
DI Notioloclinus	callytharreae	152, 154, 162	2?1000?010NN??150N0010N21NNNNN0100101000	N 1	37	20000NN00030100	N NNO	N	0NN300?1010???
DI Paracatillocrinus	granulatus	144, 146	2?1?00001????150N0010N2?NNNNN0000101000	N 1	24	2?00?7?00020100	N NN?	N	0NN?200?7?????
DI Synbathocrinus	campanulatus	144, 152	2?1?00001????150N0000N2?NNNNN0101501000	N 1	5	00000NN00010100	N NNO	N	0NN300?7?????
DI Taucatillocrinus	cephalonus	162	211000?010NN??150N0010N21NNNNN0200100000	N 1	22	20000NN00020100	N NNO	N	0NN300?10100???
Permian-3									
MO Neocamptocrinus	bundanoensis	164	200001?02110??151110000N220NNNNN120?400000	N 1	10	0?101?7?00000101	2 11?	?	0NN?200NNNN00
FL Trinalicrinus	tunisiensis	66	2????070????????15111000N2310N5001201401000	N 1	5	00001?0N00000100	N NNO	N	0NN000?7?????
CL Coenocystis	richardsoni	30	????????????10NN1NNNN1NON50N021150?000	N 0	N	NNNNNNNNNNNNNN00	N NNN	N	0NNNN1NNNN00
CL Embiocrinus	cherrabunensis	154	2???06?01????15111000N2500N5011200411000	N 1	5	0?101?0N00110100	N NN1	N	0NN300?7?????
CL Embryocrinus	variabilis	2, 66	2????070????????15131000N01NON5020111501000	N 0	N	NNNNNNNNNNNNNN00	N NNN	N	0NNNN1NNNN00

## APPENDIX 2: Sources for Morphological Data on Crinoid Species

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