

# The “Age of Crinoids”: A Mississippian Biodiversity Spike Coincident with Widespread Carbonate Ramps

THOMAS W. KAMMER

*Department of Geology and Geography, West Virginia University, Morgantown, WV 26506-6300,  
E-mail: tkammer@wvu.edu*

WILLIAM I. AUSICH

*Department of Geological Sciences, The Ohio State University, Columbus, OH 43210*

PALAIOS, 2006, V. 21, p. 238–248 DOI 10.2110/palo.2004.p04-47

*Crinoids reached their highest generic richness and overall abundance during the Mississippian, which thus has been dubbed the Age of Crinoids. The causes are hypothesized to be from the coincidence of two factors. First, in the wake of the Late Devonian mass-extinction event, the five major crinoid groups recovered and radiated in the Early Mississippian. The advanced cladids continued to radiate from their origin in the Early Devonian and reached a peak in the Middle Mississippian (Visean) that was not exceeded again until the Middle Pennsylvanian (Moscovian). Second, the Late Devonian mass-extinction event destroyed the extensive coral-stromatoporoid platform-edge reefs that had restricted circulation on carbonate platforms and limited the abundance of crinoids, which are stenohaline. The resulting carbonate ramps during the Mississippian had improved circulation, producing stenohaline conditions that resulted in an abundance peak for crinoids, recorded by widespread regional encrinites on multiple continents. This increased habitat space was ideal for camerate crinoids and resulted in a new radiation of camerate crinoids. The simultaneous radiation of pinnulate cladids and the short resurgence of camerates were responsible for the biodiversity spike in the Mississippian. The Age of Crinoids ended with a major drop in sea level at the end of the Mississippian as massive glaciers formed on Gondwana and epicontinental seas were drained.*

## INTRODUCTION

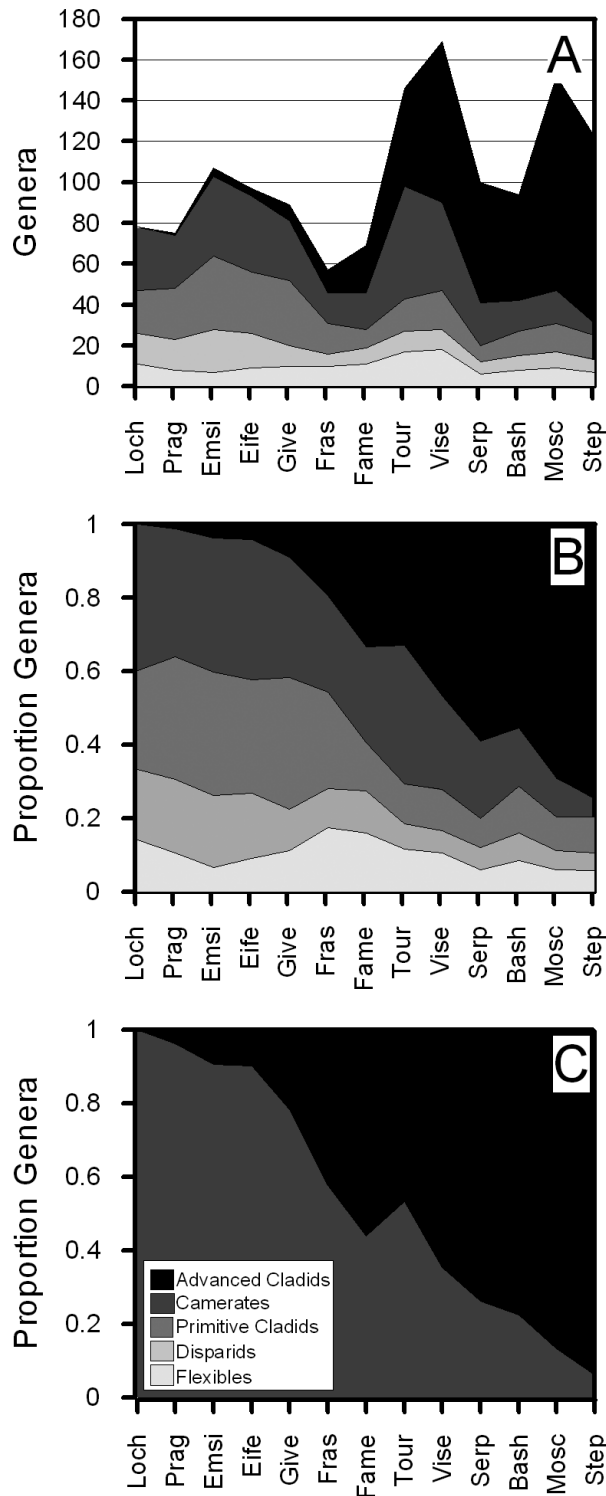
The Mississippian Period has been referred to as the Age of Crinoids (Easton, 1960; Lane, 1972; Kammer and Ausich, 1987; Levin, 1994, 1996, 1999), in reference to the simultaneously high generic richness and abundance of Mississippian crinoids. This paper considers Devonian to Pennsylvanian crinoids and offers hypotheses for the high richness and abundance of Mississippian crinoids.

High crinoid generic richness during the Mississippian is bracketed between two extinction events: the Late Devonian Frasnian–Famennian event (McGhee, 1996) and the Late Mississippian Serpukhovian event (Stanley and Powell, 2003; Fig. 1A). Between these two extinction events, crinoids reached their global maximum of Phanerozoic generic richness during the Visean Epoch (Moore and Teichert, 1978; Sepkoski, 2002). Also, during this time, there was an evolutionary transition from the Mid-

dle Paleozoic to the Late Paleozoic crinoid macroevolutionary faunas (Ausich et al., 1994; Baumiller, 1994). The Middle Paleozoic crinoid macroevolutionary fauna extended from the Early Silurian to the Middle Mississippian, and was dominated by camerates (with pinnulate arms), primitive cladids, and flexibles until the Middle Mississippian, when advanced cladids (cladids with pinnulate arms) became co-dominant with camerates. The Late Paleozoic fauna extended from the Late Mississippian to the Permian, and was dominated exclusively by advanced cladids (Fig. 1A). The other three major crinoid groups during this interval were the flexibles, primitive cladids (non-pinnulate arms), and disparids (Fig. 2). These three groups were not strongly affected during this evolutionary transition, but, instead, had a gradual decline in generic richness from the Devonian through the Pennsylvanian, with their proportions relative to one another remaining fairly static (Fig. 1A, B). Thus, the evolutionary transition is marked by a change in dominance between the two groups of pinnulate crinoids—the camerates and the advanced cladids.

## CRINOID GROUPS AND PALEOECOLOGY

Middle to Late Paleozoic crinoids comprise four groups: the subclasses Camerata, Disparida, Cladida, and Flexibilia (Ausich, 1998a, b), which are essentially clades, although the Cladida is paraphyletic because it contains the ancestors of the Flexibilia and the post-Paleozoic Subclass Articulata (Simms and Sevastopulo, 1993). Additionally, the Cladida can be divided informally into primitive cladids (Cyathocrinina and Dendrocrinina *sensu* Moore and Teichert, 1978) and advanced cladids (Poteriocrinina *sensu* Moore and Teichert, 1978) based on the first appearance of pinnules in this subclass (Kammer and Ausich, 1992, 1996). Primitive cladids first appeared in the Ordovician and are characterized by a lack of pinnules (except for the Ordovician *Eopinnacrinus*, which left no obvious descendants). In contrast, the advanced cladids, which are characterized by having pinnules, first appeared and began their radiation during the Early Devonian. Pinnules typically are small, unbifurcated branchlets that arise from each brachial of a crinoid arm. Cladids without pinnules typically had ramules, which are usually minor bifurcating or non-bifurcating branches of the arms that are more widely spaced than pinnules and do not arise from each brachial of the main arms. Thus, primitive cladids are non-pinnulate, whereas advanced cladids are pinnulate. The phylogenetic origin of pinnules within the vari-



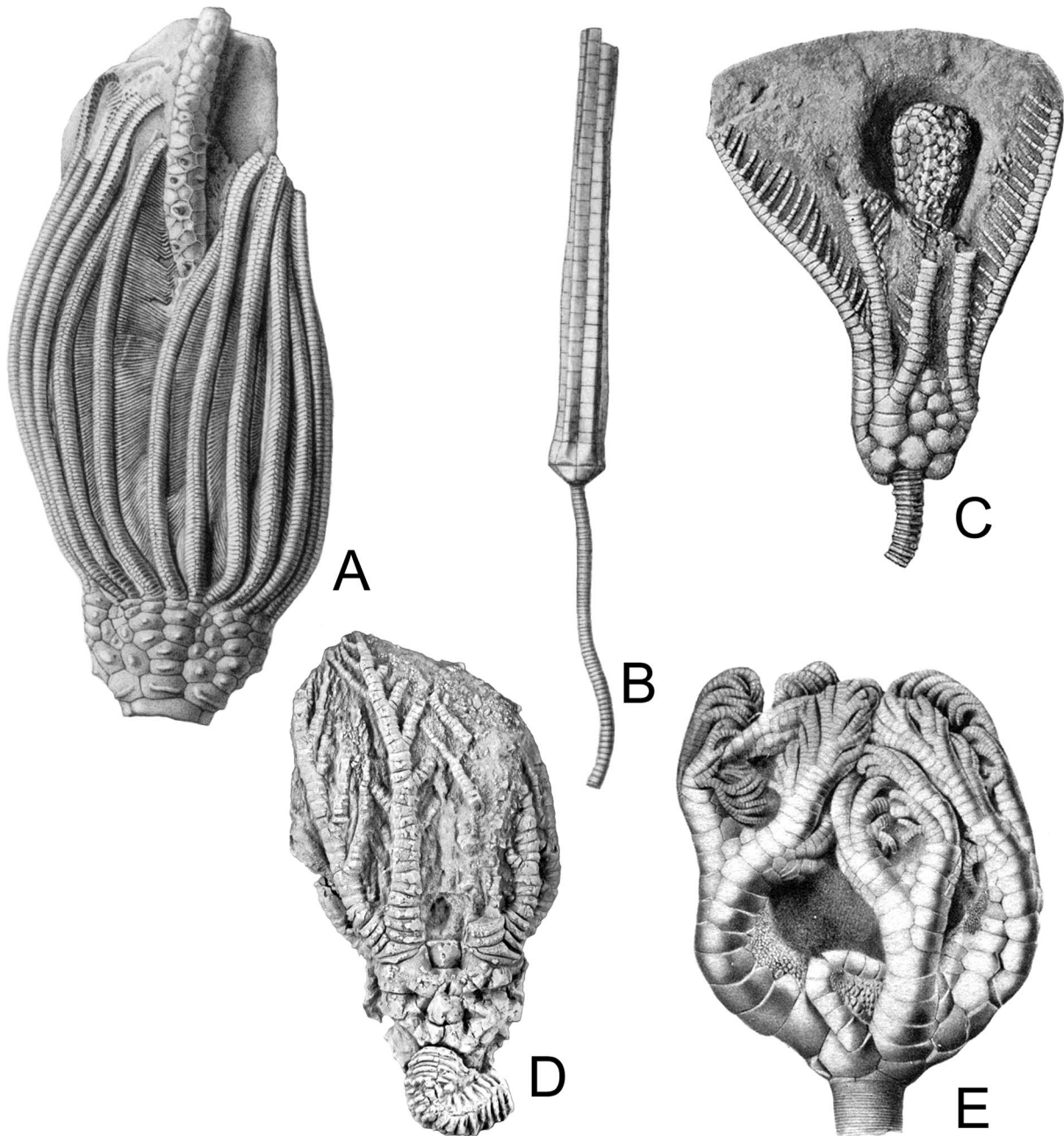
**FIGURE 1**—Plots of crinoid generic richness from revised and updated database from Sepkoski (2002) that includes 606 genera (Table 1). (A) actual generic richness; (B) proportions of the five groups relative to one another; (C) proportions of camerates and advanced cladids relative to one another; note the resurgence of camerates in the Tournaisian relative to the advanced cladids. Devonian includes Lochkovian–Famennian; Mississippian includes Tournaisian–Serpukhoviian; Pennsylvanian includes Bashkirian–Stephanian.

ous superfamilies of the advanced cladids is not well understood, but McIntosh (2001) presented evidence for the polyphyletic origin of pinnulate cladids, grouped into the Poteriocrinina (*sensu* Moore and Teichert, 1978), from within the Dendrocrinina (*sensu* Moore and Teichert, 1978). Phylogenetic practice now places the Dendrocrinina and Poteriocrinida together in the Order Dendrocrinida (Ausich, 1998b; McIntosh, 2001). Nevertheless, the functional morphology of primitive and advanced cladids differed, as discussed below, and had an impact on the evolutionary history of the Cladida, as will be shown.

Camerates and advanced cladids both possessed pinnules on the arms, whereas the disparids, primitive cladids, and flexibles all lacked pinnules, but typically had ramules (Fig. 2). These five groups represent distinct body plans among Paleozoic crinoids that are related to differences in feeding ecology (Ausich, 1980; Kammer and Ausich, 1987; Baumiller, 1993). Pinnulation produces a more-dense filtration fan than the ramulate or non-branching arms of other crinoids. Camerates and advanced cladids with pinnulate arms had the narrowest food grooves, and fed on smaller plankton, presumably phytoplankton. Disparids, primitive cladids, and flexibles had wider food grooves that presumably allowed them to feed on a wider range of plankton size, including zooplankton. These different crinoids partitioned niches by food-size selection using aerosol suspension feeding (Ausich, 1980; Kammer, 1985). Current velocity also played an important role in niche definition—pinnulate camerate and advanced cladid crinoids had clear preferences for benthic environments with strong current velocities, whereas non-pinnulate disparids and primitive cladid crinoids had no clear preference for current velocities, and were generalists (Kammer et al., 1997, 1998). In the Mississippian, these four groups were common in both siliciclastic and carbonate facies, although camerates preferred carbonate facies and were limited in siliciclastic facies, whereas advanced cladids were more characteristic of high-energy siliciclastic facies (Kammer and Ausich, 1987). Mississippian flexible crinoids were the most restricted in distribution. They preferred siliciclastic facies, with their greatest species richness in deeper-water environments, and they were relatively rare in shallow-water carbonate environments (Kammer et al., 1997, 1998).

#### CRINOID RICHNESS PATTERNS

Sepkoski's (2002) compendium of fossil marine animal genera was used as a starting point to tabulate global crinoid generic richness for the Paleozoic, although only data for the Devonian through the Pennsylvanian are presented (Fig. 1; Table 1). Range data were compiled using the range-through method (in which a genus is counted as occurring in all stages between its first and last occurrences even if there are gaps in its record), and ranges were resolved only to the stage level to minimize range uncertainty. Sepkoski's (2002) compendium lacks new crinoid data since 1998 and is incomplete for a few years prior to that date, so it was updated by consulting the crinoid literature for the period from 1996–2004 (see Table 1 for references), and by checking the ranges for all Devonian through Pennsylvanian genera using Webster (2003). Generic ranges also were checked against those in several taxo-



**FIGURE 2**—Mississippian (Visean) examples of the five major groups of Paleozoic crinoids; all  $\times 1.0$ , except for D, which is  $\times 0.5$ . (A) *Abatocrinus grandis* (Lyon), a camerate from the Edwardsville Formation, Crawfordsville, Indiana (Wachsmuth and Springer, 1897, pl. 27, fig. 1a); note dense, fine pinnules. (B) *Synbathocrinus swallowi* Hall, a disparid from the Harrodsburg Limestone, Canton, Indiana (Wachsmuth and Springer, 1897, pl. 8, fig. 7). (C) *Decadocrinus tumidulus* (Miller and Gurley), an advanced cladid from the Edwardsville Formation, Indian Creek, Indiana (Springer, 1926, pl. 17, fig. 6); note large, coarse pinnules. (D) *Barycrinus spectabilis* Meek and Worthen, St. Louis Limestone, Otter Creek, Illinois (Gahn and Kammer, 2002, fig. 1.15); note the ramulate arms. (E) *Onychocrinus ulrichi* Miller and Gurley, a flexible from the Edwardsville Formation, Indian Creek, Indiana (Springer, 1920, pl. 66, fig. 2); note ramulate arms.

nomic papers (Ausich and Kammer, 1990, 1991a, b, 1992; Ausich et al., 1997; Kammer and Ausich, 1992, 1993, 1994, 1996; Gahn and Kammer, 2002; Kammer and Gahn, 2003; Lee et al., 2005), as well as a database of Mississippian crinoids from Western Europe that the authors have compiled. The revised database consists of 606 genera, which includes: addition of 50 new genera, deletion of 13 genera that were either junior synonyms or columnal taxa, net extension of three Silurian genera into the Devonian, and

range revisions for 137 genera. Most of the range revisions corrected first or last occurrences by only a single stage, although a minority of genera had range revisions encompassing several stages. Devonian ranges were standardized using Bultynck (2000). An Appendix with the complete database of generic ranges in Microsoft Excel® format is available electronically at <http://www.sepm.org/archive/index.html>.

Recent studies on the fidelity of data in the Sepkoski

**TABLE 1**—Crinoid generic richness for the Lower Devonian–Upper Pennsylvanian based on Sepkoski's (2002) compendium (in parentheses) plus updates from the following references: Arendt, 1997, 2002; Ausich and Sevastopulo, 2001; Chen et al., 1997; Harvey and Ausich, 1997; Jell, 1999; Jell and Jell, 1999; Jell and Theron, 1999; Itano et al., 2003; Lane et al., 1996, 2001a, b; McIntosh, 2001; Prokop, 2002; Waters et al., 2003; Webster, 1997, 2001, 2003; Webster and Jell, 1999a; Webster et al., 2003, 2004. Devonian includes Lochkovian–Famennian; Mississippian includes Tournaisian–Serpukhovian; Pennsylvanian includes Bashkirian–Stephanian.

Stage	Advanced cladids	Camerates	Primitive cladids	Disparids	Flexibles	Totals
Stephanian	91 (89)	6 (6)	12 (11)	6 (5)	7 (6)	122 (117)
Moscovian	105 (100)	16 (13)	14 (11)	8 (6)	9 (6)	152 (136)
Bashkirian	52 (50)	15 (9)	12 (11)	7 (5)	8 (5)	94 (80)
Serpukhovian	59 (53)	21 (14)	8 (8)	6 (5)	6 (5)	100 (85)
Visean	79 (76)	43 (52)	19 (22)	10 (9)	18 (16)	169 (175)
Tournaisian	48 (34)	55 (49)	16 (16)	10 (9)	17 (13)	146 (121)
Famennian	23 (8)	18 (9)	9 (9)	8 (6)	11 (8)	69 (40)
Frasnian	11 (11)	15 (14)	15 (14)	6 (7)	10 (9)	57 (55)
Givetian	8 (8)	29 (33)	32 (25)	10 (14)	10 (11)	89 (91)
Eifelian	4 (3)	37 (42)	30 (27)	17 (21)	9 (9)	97 (102)
Emsian	4 (4)	39 (46)	36 (32)	21 (22)	7 (5)	107 (109)
Pragian	1 (0)	26 (19)	25 (20)	15 (15)	8 (6)	75 (60)
Lochkovian	0 (0)	31 (22)	21 (16)	15 (13)	11 (9)	78 (60)

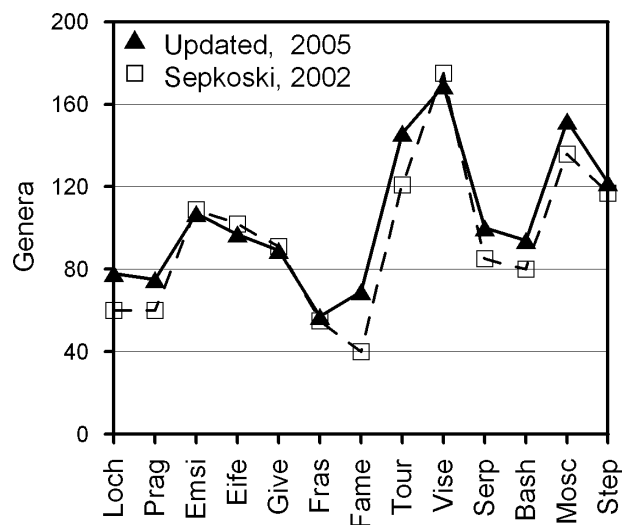
compendium have identified errors both intrinsic and extrinsic to the compendium, and have concluded either that errors are random, and therefore not significant, or that they are non-random, with a significant impact. Intrinsic errors include: taxonomic inaccuracies (Culver et al., 1987; Adrain and Westrop, 2000; Smith and Jeffrey, 2000; Alroy, 2002, Ausich and Peters, 2005), inaccurate first and/or last occurrences (Adrain and Westrop, 2000; Smith and Jeffrey, 2000; Jeffrey, 2001; Ausich and Peters, 2005), and uneven sampling of the fossil record (Miller and Foote, 1996; Alroy et al., 2001). By verifying and updating Devonian through Pennsylvanian crinoid genera from the Sepkoski (2002) compendium, obvious intrinsic errors and omissions have been corrected. At this time, uneven sampling and the various extrinsic biases have not been evaluated for the revised data. Potential extrinsic biases include: the total area of sedimentary rock available for sampling (Raup, 1976; Smith, 2001; Peters and Foote, 2001, 2002), geographic and paleoenvironmental variation in the rock record (Ronov, 1978; Ronov et al., 1980; Allison and Briggs, 1993; Smith et al., 2001), and taphonomic considerations (Cherns and Wright, 2000; Donovan, 2001; Wright et al., 2003). One or more of these factors certainly could be affecting temporal trends, but, for the following reasons, they are regarded to have been minimal, especially for the broad richness patterns considered here: (1)

**TABLE 2**—Comparison of Sepkoski's (2002) original data (up to 1998) with the revised data for the Devonian through Carboniferous. The revised database includes: 50 new genera, 13 genera removed as junior synonyms or stem taxa, a net of three Silurian genera extended into the Devonian, and 137 genera with range revisions.

	Sepkoski, 2002 (No. genera)	Revised database (No. genera)
Camerates	158	165
Disparids	55	56
Primitive Cladids	81	95
Advanced Cladids	230	249
Flexibles	41	41
Totals	566	606

trends are evaluated only at the stage level; and (2) the majority of data are derived from crinoid Lagerstätten, so data are from similar taphonomic windows, and most record once-living communities, preserving the actual relative proportions of taxa.

The overall pattern derived from Sepkoski's (2002) compendium is substantially the same as that of the revised database (Table 2, Fig. 3), although there are some distinct differences at the stage level, particularly for the Famennian where richness increased by 73% because of recent work by Lane et al. (2001a, b) and Waters et al. (2003). However, these stage-level differences have little effect on recognition of the Mississippian richness peak and the stage-level patterns described here.



**FIGURE 3**—Comparison of data from Sepkoski (2002) with the total revised database using references listed in Table 1. The pattern of total generic richness for the Devonian through Pennsylvanian is substantially the same for both data sets, although there clearly are some differences at the stage level, particularly the 73% increase in the Famennian. Devonian includes Lochkovian–Famennian; Mississippian includes Tournaisian–Serpukhovian; Pennsylvanian includes Bashkirian–Stephanian.

Data are presented in terms of both absolute generic richness and proportion of generic richness (Table 1, Fig. 1). Figure 1 shows how the proportions of the various crinoid groups changed over time. Several clear patterns are apparent in the data:

- (1) there were three generic richness peaks (Fig. 1A), including the Emsian (Devonian), Visean (Mississippian), and Moscovian (Pennsylvanian). Crinoid richness peaked during the Early Devonian and declined to a minimum by the Frasnian. Crinoid richness began to recover in the Famennian, rapidly increased during the Tournaisian, peaked in the Visean, and declined again in the Serpukhovian. Richness recovered by the Moscovian (Middle Pennsylvanian), at which time the advanced cladids were overwhelmingly dominant.
- (2) Advanced cladids first appeared during the Pragian (Table 1) and steadily increased in their proportion of the crinoid faunas through the Pennsylvanian (Fig. 1B). Advanced cladids achieved a local richness maximum during the Visean (79), which was not exceeded again until the Moscovian (105) (Table 1).
- (3) Flexibles, disparids, and primitive cladids were smaller groups that maintained fairly stable levels of richness in terms of both their absolute richness (Fig. 1A) and their proportions relative to one another (Fig. 1B), although they slowly declined in absolute richness over the study interval.
- (4) Camerates, the dominant group during the Devonian, decreased steadily as a proportion of the crinoid faunas during the Mississippian and the Pennsylvanian, whereas the advanced cladids were simultaneously increasing as a proportion of the faunas (Fig. 1B, C). Regardless, camerates reached a richness maximum during the Tournaisian (55), which exceeded the Devonian maximum (Emsian, 39) (Table 1). This Tournaisian peak represents the maximum richness for camerates, and is matched only by the 55 camerate genera of the Wenlock (Silurian) (Sepkoski, 2002).

#### RISE OF ADVANCED CLADIDS AND FALL OF CAMERATES

The advanced cladids ultimately were the successful Paleozoic group. They gave rise to the Subclass Articulata (all post-Paleozoic crinoids) (Simms and Sevastopulo, 1993; Hess et al., 1999) at or before the end-Permian extinction event (Webster and Jell, 1999b).

The transition in the dominant type of pinnulated crinoid (camerate to advanced cladids) occurred during the Middle to Late Mississippian—an interval of major environmental change in at least North America and Europe. During this time, carbonate settings were being replaced by prograding siliciclastics resulting from the orogenies associated with the assembly of Pangea, such as the 300–340 Ma Hercynian Orogeny in Europe (Windley, 1984), the initial stages of the Alleghanian Orogeny in eastern North America (Chesnut, 1991; Etensohn, 1994), the Antler Orogeny in western North America (Sloss, 1988; Burchfiel and Royden, 1991), and the eustatic drop in sea level associated with Gondwanan glaciers (Stanley and Powell, 2003). The widespread carbonate ramps of the Tournaisian and Visean were replaced by cyclic sequences

of thick siliciclastics and thin carbonates during the Namurian to Stephanian in much of North America and Europe (Veevers and Powell, 1987; Sloss, 1988; Leeder, 1992; Smith and Read, 2000; Read et al., 2002).

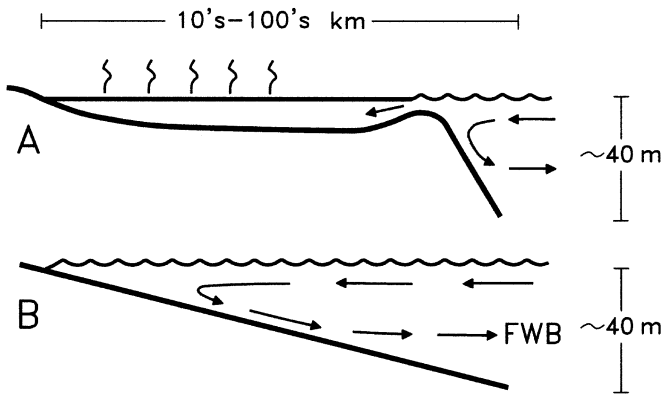
#### Devonian

A peak in generic richness occurred during the Emsian (Fig. 1A). The Early Devonian also was the time when pinnulate advanced cladids originated. Advanced cladids were the only Paleozoic crinoids that evolved muscular articulations between arm plates, including brachials and pinnules (Ubaghs, 1978; Ausich and Baumiller, 1993). Other crinoids had only ligamentary articulations. Muscular articulations allowed for relatively rapid, active movement of the arms, pinnules, and even, indirectly, the crown, rather than the passive or, perhaps, very slow movement of a crinoid with only ligamentary connective tissue in the arms (Wilkie, 1984). One important advantage of these crinoids was that they could keep their filtration fans free from unwanted sediment easily. Kammer et al. (1998) described how modern crinoids use pinnule flicking to remove unwanted sediment particles from their filtration fan (in this case, from the prop wash of a submersible). This ability may explain why advanced cladids were specialized for higher-turbidity siliciclastic settings where the dense fan of camerates would be fouled more easily with sediment (Kammer and Ausich, 1987; Kammer et al., 1998). Thus, the gradual replacement may reflect the gradual encroachment of siliciclastic environments (Ausich et al., 1979; Matchen and Kammer, 1994; Richardson and Ausich, 2004).

The Frasnian–Famennian mass extinction was a significant event for many major groups of marine invertebrates (McGhee, 1996), and crinoids were not an exception. Generic richness at the end of the Frasnian was at the lowest level for the entire Devonian to Pennsylvanian interval with the absolute number of camerates and primitive cladids being affected the most, although advanced cladids increased in richness during this time (Table 1). However, no drastic change occurred in the proportions of the various groups during this time (Fig. 1B). Although crinoid richness plummeted during the Frasnian in North America and Europe, many groups apparently survived in refugia, such as in China (Lane et al., 1997) or Europe (Lane et al., 2001a, b). Waters et al. (2003) even reported that Chinese Famennian crinoids have a Carboniferous aspect, and are unlike typical Devonian faunas, hypothesizing they may have sourced the Early Carboniferous radiation. The initial recovery in crinoid generic richness in the Famennian supports this hypothesis (Fig. 1A).

#### Mississippian: The Age of Crinoids

Crinoids were not only diverse during the Mississippian, they were also very abundant, forming the familiar Mississippian encrinites. Encrinites are defined as >50% crinoidal grainstones and packstones. Globally, during the Early to Middle Mississippian, many encrinites were so thick and geographically extensive that they have been termed regional encrinites (Ausich, 1997; Phelps et al., 2003). The Burlington and Keokuk limestones of the U.S. Midcontinent exemplify the regional encrinite facies, and



**FIGURE 4**—Circulation on a carbonate platform versus carbonate ramp. (A) Platform-edge reef system restricts circulation on the inner platform; evaporation increases salinity. (B) Carbonate ramp lacks a platform-edge reef system resulting in more-open circulation and stenohaline conditions. FWB: fair-weather wave base.

extend over 74,000 km<sup>2</sup> of outcrop, with a combined thickness exceeding 50 m (Ausich, 1997). Mississippian regional encrinites occur throughout North America, Europe, North Africa, and central Asia (Ausich, 1997; Webster et al., 2003).

This high abundance and maximum richness of crinoids coincided with a significant crinoid faunal change during the middle Visean. The middle Visean change was so profound that it was once thought to represent a mass-extinction event at the Osagean–Meramecian stage boundary (Laudon, 1948; Lane, 1972). However, rather than being an abrupt extinction event, this faunal change was one of continual faunal turnover at the substage level (Ausich et al., 1994) during the transition from the Middle to the Late Paleozoic crinoid macroevolutionary fauna. This overlap of two macroevolutionary faunas accounts for the high crinoid richness. Beginning in the Givetian, the radiation of pinnulate cladids was coincident with a loss in camerate generic richness. However, the opening of new, expansive carbonate-ramp settings—an ideal camerate crinoid habitat—propagated renewed diversification of camerate crinoids during the Tournaisian and Visean. It is this renewed diversification of elements of the Middle Paleozoic crinoid fauna, coincident with the continued radiation of the pinnulate cladids of the Late Paleozoic crinoid fauna, which is hypothesized to have resulted in the Visean biodiversity spike in crinoids.

Clearly, conditions were optimal for crinoids during this time. Crinoids are stenohaline animals that depend on currents to supply them with food (Fell, 1966; Meyer, 1973). The Frasnian–Famennian mass extinction of coral-stromatoporoid reefs had wiped out a reef ecosystem with an areal extent nearly ten times greater than modern reefs (Copper, 1994, 2002). Without platform-edge reefal buildups in the Early Mississippian (Webb, 2002), open-marine circulation would have extended more readily across shallow-water carbonate facies, producing carbonate ramps instead of reef-rimmed platforms (Fig. 4). During the Mississippian, carbonate ramps were the dominant setting for carbonate accumulation (Wright and Faulkner, 1990). The Mississippian was “truly the time of ramps” (Ahr, 1989, p. 211). In fact, carbonate accumula-

tion reached a Phanerozoic maximum (matched only during the Middle Cambrian) during the Mississippian that was twice as high as the next highest younger peak in the Late Cretaceous (Walker et al., 2002, fig. 3). In general, the Tournaisian and Visean in North America and Europe was a time of tectonic quiescence when carbonate deposition was widespread between Late Devonian and Late Mississippian siliciclastic wedges (Sloss, 1988; Leeder, 1992; Ettensohn et al., 2002). A notable exception was the progradational Borden Delta, which, in combination with coeval carbonate facies, fortuitously provided the opportunity to identify the paleoenvironmental preferences of Early Mississippian crinoid clades (Kammer and Ausich, 1987; Kammer et al., 1998).

Crinoids were well adapted to reefs during the Paleozoic, and continue into the oceans of today (Lowenstam, 1957; Lane, 1971; Meyer, 1985; Bradbury et al., 1987). However, the presence of a rimmed platform bordering an epicontinental sea may have produced a circulation restriction that significantly affected the paleoceanography of the epicontinental sea. In many instances, with rimmed shelves, normal-marine conditions would be at the reef belt along the platform margin and a relatively short distance landward. Because of this restriction, the salinity of the more landward portion of the platform would be other than normal-marine conditions in many cases, depending on various climatic, paleogeographic, and other factors. In contrast, in most cases, a carbonate ramp provided a relatively expansive area where normal-marine salinities would be expected to be maintained over an extensive area (Fig. 4).

The potential for restricted circulation to yield changes in ocean chemistry is demonstrated by the present Bahama and Florida platforms and Ordovician epicontinental seas. Oceanic circulation is sufficiently interrupted today so that waters on the Great Bahama Bank on the western side of Andros Island experience summertime hypersalinity up to 45‰ (Bathurst, 1976). Similarly,  $\delta^{13}\text{C}$  values vary as much as 4.0‰ in Florida Bay and Bahamian platforms as compared to the open ocean (Patterson and Walter, 1994). Bowersox (2005) documented salinity-induced forcing of faunal patterns in a Pliocene silled basin in California. Both the modern Bahamas and the Pliocene of California are small in areal extent when compared to epicontinental seas. The much larger extent of epicontinental seas should have magnified these circulation affects. Recent work shows how the chemistry of a large Paleozoic epicontinental sea was affected by distance from shoreline. Sea-ocean chemistry changed as a function of on-shore-offshore distance, source of freshwater, etc. during the Ordovician, and aquafacies have been defined on the basis of differing concentrations of C, O, and Nd isotopes (Holmden, et al., 1998; Young et al., 2005). Additionally, the composition of Mississippian and Pennsylvanian communities in the Appalachian Basin was controlled by salinity gradients (Kammer and Lake, 2001; Lebold and Kammer, 2006). Extreme hypersalinity is well known from the Silurian and Devonian when basin centers underwent major episodes of evaporite deposition (Copper, 2002). Thus, the concept of restricted waters in epicontinental seas landward of rimmed platforms is feasible.

Extreme salinities are not needed to restrict crinoids in today's oceans. The slight salinity elevations present on

the Great Bahama Bank, as noted above, are lethal to modern crinoids (Fell, 1966), and crinoids are not present on the extensive bank on the western side of Andros Island (Zeiller, 1974). In contrast, four species of shallow-water comatulid crinoids are present on the Little Bahama Bank on the south side of Grand Bahama Island where it faces the open ocean (Macurda, 1973).

Modern crinoids have a porous tegmen, through which sea water is free to enter the body, making them susceptible to osmotic shock (Meglitsch, 1972). Many fossil crinoids also had a porous tegmen (Springer, 1900). Echinoderms in general have little ability to control the movement of water or salts through their cell walls (Meglitsch, 1972), and, thus, have a more limited salinity range than many other invertebrates. Experiments by Clark (1921) indicate that crinoids can tolerate salinities between 24–36‰, but under natural conditions, they are restricted to normal marine environments (Fell, 1966).

Non-reefal carbonate buildups, most notably Waulsortian mounds, did occur during the Early Mississippian (Lees and Miller, 1995). These microbial mounds formed in outer-ramp settings in the absence of skeletal framework reefs (Wright and Faulkner, 1990; Walker et al., 2002). The mounds afforded a new facies for crinoids by creating a perch for them in an offshore setting. The abundant and diverse crinoid faunas of Clitheroe, England lived on Waulsortian mounds (Bowden et al., 1997), as did other crinoid faunas in Ireland, New Mexico, Montana, and other sites (Bolton et al., 1982).

Crinoids flourished on Early Mississippian carbonate ramps, peaking during the Visean. Although Visean crinoid associations commonly include representatives from all groups, camerates typically dominated in carbonate settings, and advanced cladids dominated in siliciclastic settings (Kammer and Ausich, 1987; Kammer et al., 1998). Disparid and primitive cladid crinoids had relatively constant richness through the Mississippian, perhaps because they were eurytopic (but not euryhaline), which allowed them to inhabit a wide array of marine (stenohaline) environments (Kammer et al., 1997, 1998). The reason for the relative stability of the flexibles is less clear, but their specialization for deep-water environments (Kammer et al., 1997, 1998) apparently afforded them extinction resistance during this time interval.

#### Serpukhovian Extinction: End of the Age of Crinoids

The Serpukhovian extinction event ended the Mississippian Age of Crinoids. This coincides with fluctuations in sea level during the Late Mississippian as glaciers waxed and waned on Gondwana (Smith and Read, 2000). Gondwanan glaciers reached massive size by the end of the Serpukhovian, with a major eustatic drop in sea level (Stanley and Powell, 2003) and greatly reduced area of tropical-marine shelves. Whether this extinction event was prolonged or abrupt for crinoids is difficult to determine because of the extensive and widespread Mississippian–Pennsylvanian unconformity in North America (Sloss, 1963, 1988; Saunders and Ramsbottom, 1986) and the nearly complete lack of crinoids from the Serpukhovian–Bashkirian boundary in western Europe (Bassler and Moodey, 1943; Wright, 1950, 1951a, b, 1952, 1954, 1955a, b, 1956, 1958, 1960). When sea level rose again, renewed

siliciclastic input to marine environments occurred, resulting from orogenies associated with the assembly of Pangea (Windley, 1984). Crinoids that could tolerate siliciclastic influx better, the advanced cladids, increased in proportion during the Serpukhovian, then dominated in the remainder of the Paleozoic (Fig. 1B, C).

#### DISCUSSION AND CONCLUSIONS

The acme of Phanerozoic crinoid richness and abundance was reached during the Visean Epoch of the Mississippian Period. The causes were undoubtedly complex, but the coincidence of two factors may have played a major role. The first factor was the rising biodiversity peak of advanced cladids during the transition from the Middle Paleozoic to the Late Paleozoic Crinoid Macroevolutionary Fauna. The second factor was the establishment of widespread carbonate ramps following the Late Devonian extinction of coral-stromatoporoid framework reefs, which facilitated a camerate radiation. Although camerate dominance was waning in the Late Devonian, they had a brief, renewed radiation on carbonate ramps. Carbonate ramps were ideal for camerates, where they became exceedingly abundant and diverse. Carbonate ramps not only were favorable for camerate crinoids, but this habitat covered extensive areas. Thus, the increase in abundance and diversity may be explained by the species-area curves of Island Biogeography Theory (MacArthur and Wilson, 1967).

The improved circulation on carbonate ramps may have allowed more extensive colonization of benthic substrates by these stenohaline animals than was possible with the restricted circulation that may have been typical on back-reef platforms of the Devonian (Fig. 4). The much smaller number of encrinites during the Devonian, as compared to the Mississippian (Ausich, 1997), strongly suggests some limiting factor for crinoids, possibly normal-marine salinity. Slight increases or decreases in salinity, but not enough to produce evaporite deposits or even restrict other common benthic invertebrates, such as brachiopods and bryozoans, may have restricted crinoids. In the Great Bahama Bank example cited above, a wide variety of benthic marine invertebrates exist, yet its elevated summer salinities (Bathurst, 1976) may be the reason comatulid crinoids are absent, even though asteroids, ophiuroids, and echinoids are common (Zeiller, 1974), all of which can tolerate a greater range of salinities (Booolootian, 1966). In contrast, comatulids are common on reef fronts and platforms facing the open ocean in the Caribbean (Macurda, 1973; Meyer, 1973; Macurda and Meyer, 1983), and are common on reefs of the western Pacific (Meyer and Macurda, 1980; Bradbury et al., 1987). Reef-front environments provide the normal-marine salinities required by crinoids and provide currents to help optimize feeding (Meyer, 1997). Reef environments, as opposed to back-reef environments, long have been a preferred habitat for crinoids (Lowenstam, 1957; Lane, 1971).

The change in dominance between camerates and advanced cladids began during the Visean as crinoid faunas were changing across the Osagean–Meramecian boundary (Ausich et al., 1994), and accelerated during the Serpukhovian (Table 1). This changeover is thought to reflect the adaptation of advanced cladids to higher turbidity, analogous to that seen in the Late Devonian. Alternative-

ly, Waters and Maples (1991) hypothesized that this was primarily a predation-mediated faunal change. They cited the ideas of Lane (1984), who proposed that the advanced cladid design had predation resistance because the anal sac (Fig. 2C), which contained the highly nutritious gonads, could be cropped by a predator without the destruction of the calyx, thus allowing the animal to survive. In contrast, predation on camerate gonads would be lethal as they were contained in the calyx.

Predation was a very important factor in crinoid evolution and has been hypothesized to be responsible for the Middle Paleozoic Marine Revolution, where crinoids developed more spines and thicker calyx plates (Signor and Brett, 1984), and the present bathymetric restriction of isocrinids to deep water and the associated adaptive radiation of comatulids in shallow water (Meyer and Macurda, 1977; Baumiller and Gahn, 2003). Was the change in dominance from camerates to advanced cladids during the Mississippian the result of predation? Baumiller and Gahn (2004) documented arm-regeneration in 11 Paleozoic crinoid Lagerstätten in order to quantify predation intensity. They found a statistically significant increase in the frequency of arm regeneration from 3.1% to 12.4% between the Silurian and Devonian, but no significant increase in either the Mississippian or Pennsylvanian, where regeneration rates were 12.8% and 10.5%, respectively. The increase from the Silurian to the Devonian represents the Middle Paleozoic Marine Revolution. The data for the Mississippian and Pennsylvanian do not support the hypothesis of increased predation as a causal factor for the change in dominance between camerates and advanced cladids. The predation rates for both the Devonian and Mississippian were essentially identical, with camerates comprising 83% of the Devonian data and 85% of the Mississippian data.

Whereas evidence in support of a predation-mediated change may yet be found, it appears more likely that environmental change was the primary factor in the turnover of pinnulate crinoids. This transition occurred over a period of approximately 70 million years, from the Early Devonian to the Late Mississippian, as advanced cladids slowly increased in diversity until they were the dominant crinoid group. The major shift in dominance took place during the Middle to Late Mississippian when there was a transition from carbonate-dominated to siliciclastic-dominated settings (Windley, 1984; Sloss, 1988; Leeder, 1992; Smith and Read, 2000; Etnesoehn et al., 2002).

Ultimately, the transition led to a change of dominance from one pinnulate clade to another. The expansion of the advanced cladids indicates an adaptive radiation apparently made possible by the evolutionary innovation of muscular arms. Whereas it might be tempting to infer that this pattern represents competitive replacement of the camerates by the advanced cladids, their respective preferences for different environments suggests they generally avoided direct competition. The richness peak for both groups in the Visean also indicates a peaceful coexistence between these two groups when conditions for crinoids apparently were better than at any other time during the Phanerozoic.

#### ACKNOWLEDGEMENTS

This research was supported by the National Science Foundation: EAR-0206307 (TWK) and EAR-02059068

(WIA). D. Vesper drafted Figures 1 and 3. G.D. Webster, J.A. Waters, M. Foote, and an anonymous reviewer provided careful reviews that improved earlier drafts of the manuscript.

#### REFERENCES

- ADRAIN, J.M., and WESTROP, S.R., 2000, An empirical assessment of taxic paleobiology: *Science*, v. 289, p. 110–112.
- AHR, W.M., 1989, Sedimentary and tectonic controls on the development of an Early Mississippian carbonate ramp, Sacramento Mountains area, New Mexico: *in* Crevello, P.D., Wilson, J.L., Sarg, J.F., and Read, J.F., eds., *Controls on Carbonate Platform and Basin Development*: Society of Economic Paleontologists and Mineralogists Special Paper 44, p. 203–212.
- ALLISON, P.A., and BRIGGS, D.E.G., 1993, Exceptional fossil record; distribution of soft-tissue preservation through the Phanerozoic: *Geology*, v. 21, p. 527–530.
- ALROY, J., 2002, How many named species are valid?: *Proceedings of the National Academy of Sciences of the United States of America*, v. 99, p. 3706–3711.
- ALROY, J., MARSHALL, C.R., BAMBACH, R.K., BEZUSKO, K., FOOTE, M., FÜSICH, F.T., HANSEN, T.A., HOLLAND, S.M., IVANY, L.C., JABLONSKI, D., JACOBS, D.K., JONES, D.C., KOSNIK, M.A., LIDGARD, S., LOW, S., MILLER, A.I., NOVACK-GOTTSHALL, P.M., OLSZEWSKI, T.D., PATZKOWSKY, M.E., RAUP, D.M., SEPKOSKI, J.J., JR., SOMMERS, M.G., WAGNER, P.J., and WEBBER, A., 2001, Effects of sampling standardization on estimates of Phanerozoic marine diversity: *Proceedings of the National Academy of Sciences of the United States of America*, v. 98, p. 6261–6266.
- ARENDRT, YU. A., 1997, New Carboniferous crinoids with four–six arms from the Moscow region: *Paleontological Journal*, v. 31, p. 400–408.
- ARENDRT, YU. A., 2002, Early Carboniferous echinoderms of the Moscow region: *Paleontological Journal*, v. 36, Supplement 2, p. 115–184.
- AUSICH, W.I., 1980, A model for niche differentiation in Lower Mississippian crinoid communities: *Journal of Paleontology*, v. 54, p. 273–288.
- AUSICH, W.I., 1997, Regional encrinites: a vanished lithofacies: *in* Brett, C.E., and Baird, G.C., eds., *Paleontological Events, Stratigraphic, Ecological, and Evolutionary Implications*: Columbia University Press, New York, p. 509–519.
- AUSICH, W.I., 1998a, Early phylogeny and subclass division of the Crinoidea (Phylum Echinodermata): *Journal of Paleontology*, v. 72, p. 499–510.
- AUSICH, W.I., 1998b, Phylogeny of Arenig to Carodoc crinoids (Phylum Echinodermata) and suprageneric classification of the Crinoidea: *The University of Kansas Paleontological Contributions*, New Series, No. 9, 36 p.
- AUSICH, W.I., and BAUMILLER, T.K., 1993, Taphonomic method for determining muscular articulations in fossil echinoderms: a test for the occurrence of muscles in Lower Mississippian cladid crinoids: *PALAIOS*, v. 8, p. 477–484.
- AUSICH, W.I., and KAMMER, T.W., 1990, Systematics and phylogeny of the late Osagean and Meramecian crinoids *Platycrinites* and *Eucaladocrinus* from the Mississippian stratotype region: *Journal of Paleontology*, v. 64, p. 759–778.
- AUSICH, W.I., and KAMMER, T.W., 1991a, Late Osagean and Meramecian *Actinocrinites* (Echinodermata: Crinoidea) from the Mississippian stratotype region: *Journal of Paleontology*, v. 65, p. 485–499.
- AUSICH, W.I., and KAMMER, T.W., 1991b, Systematic revisions to *Aorocrinus*, *Dorycrinus*, *Macrocrinus*, *Paradihocrinus*, *Strotocrinus*, and *Uperocrinus*: Mississippian camerate crinoids (Echinodermata) from the stratotype region: *Journal of Paleontology*, v. 65, p. 936–944.
- AUSICH, W.I., and KAMMER, T.W., 1992, *Dizygocrinus*: Mississippian camerate crinoid (Echinodermata) from the midcontinental United States: *Journal of Paleontology*, v. 66, p. 637–658.
- AUSICH, W.I., KAMMER, T.W., and BAUMILLER, T.K., 1994, Demise of



- the middle Paleozoic crinoid fauna: a single extinction event or rapid faunal turnover?: *Paleobiology*, v. 20, p. 345–361.
- AUSICH, W.I., KAMMER, T.W., and LANE, N.G., 1979, Fossil communities of the Borden (Mississippi) Delta in Indiana and northern Kentucky: *Journal of Paleontology*, v. 53, p. 1182–1196.
- AUSICH, W.I., KAMMER, T.W., and MEYER, D.L., 1997, Middle Mississippian disparid crinoids from the midcontinental United States: *Journal of Paleontology*, v. 71, p. 131–148.
- AUSICH, W.I., and PETERS, S.E., 2005, A revised macroevolutionary history for Ordovician–Early Silurian crinoids: *Paleobiology*, v. 31, p. 538–551.
- AUSICH, W.I., and SEVASTOPULO, G.D., 2001, The Lower Carboniferous (Tournaisian) crinoids from Hook Head, County Wexford, Ireland: *The Palaeontological Society Monograph*, v. 216, p. 1–136.
- BASSLER, R.S., and MOODEY, M.W., 1943, Bibliographic and faunal index of Paleozoic pelmatozoan echinoderms: *Geological Society of America Special Paper*, 45, 734 p.
- BATHURST, R.G.C., 1976, *Carbonate Sediments and Their Diagenesis: Developments in Sedimentology 12*, Elsevier, Amsterdam, 658 p.
- BAUMILLER, T.K., 1993, Survivorship analysis of Paleozoic Crinoidea: effect of filter morphology on evolutionary rates: *Paleobiology*, v. 19, p. 304–321.
- BAUMILLER, T.K., 1994, Patterns of dominance and extinction in the record of Paleozoic crinoids: *in* David, B., Guille, A., Feral, J.P. and Roux, M., eds., *Echinoderms Through Time*: Rotterdam, Balkema, p. 193–198.
- BAUMILLER, T.K., and GAHN, F.J., 2003, Predation on crinoids: *in* Kelley, P.H., Kowalewski, M., and Hansen, T., eds., *Predator-Prey Interactions in the Fossil Record*: Kluwer Academic/Plenum Publishers, New York, p. 263–278.
- BAUMILLER, T.K., and GAHN, F.J., 2004, Testing predator-driven evolution with Paleozoic crinoid arm regeneration: *Science*, v. 305, p. 1453–1455.
- BOLTON, K., LANE, H.R., and LEMONE, D.V., eds., 1982, *Symposium on the Paleoenvironmental Setting and Distribution of the Waulsortian Facies*: El Paso Geological Society and the University of Texas at El Paso, El Paso, 182 p.
- BOOLOOTIAN, R.A., 1966, *Physiology of Echinodermata*: Interscience Publishers, New York, 822 p.
- BOWDEN, A., WEBSTER, M., and MITCHAM, T., 1997, *Salthill Quarry Geology Trail: Geologists' Association Guide No. 58*, 30 p.
- BRADBURY, R.H., REICHEL, R.E., MEYER, D.L., and BIRTLEY, R.A., 1987, Patterns in the distribution of the crinoid community at Davies Reef on the central Great Barrier Reef: *Coral Reefs*, v. 5, p. 189–196.
- BULTYNCK, P., ed., 2000, *Subcommission on Devonian stratigraphy, recognition of Devonian series and stage boundaries in geological areas*: *Courier Forschungsinstitut Senckenberg*, v. 225, 350 p.
- BURCHFIELD, B.C., and ROYDEN, L.H., 1991, *Antler Orogeny, a Mediterranean-type orogeny*: *Geology*, v. 19, p. 66–69.
- CHEN, Z-T., WEI, W-L., and DAI, G-X., 1997, One new genus of crinoid from Lower Carboniferous of Guilin area, Guangxi, China: *Acta Palaeontologica Sinica*, v. 36, p. 52–57.
- CHERNS, L., and WRIGHT, V.P., 2000, Missing molluscs as evidence of large-scale, early skeletal aragonite dissolution in a Silurian sea: *Geology*, v. 28, p. 791–794.
- CHESNUT, D.R., JR., 1991, Timing of the Alleghanian tectonics determined by Central Appalachian foreland basin analysis: *South-eastern Geology*, v. 31, p. 203–221.
- CLARK, A.H., 1921, *A monograph of the existing crinoids*: *Bulletin of the U.S. National Museum*, 82, vol. 1, pt. 2, p. 1–795.
- COPPER, P., 1994, Ancient reef ecosystem expansion and collapse: *Coral Reefs*, v. 13, p. 3–12.
- COPPER, P., 2002, Silurian and Devonian reefs: 80 million years of global greenhouse between two ice ages: *in* Kiessling, W., Flügel, E., and Golonka, J., eds., *Phanerozoic Reef Patterns*: Society of Economic Paleontologists and Mineralogists Special Publication 72, p. 181–238.
- CULVER, S.J., BUZAS, M.A., and COLLINS, L.S., 1987, On the value of taxonomic standardization in evolutionary studies: *Paleobiology*, v. 13, p. 169–176.
- DONOVAN, S.K., 2001, Evolution of Caribbean echinoderms during the Cenozoic: moving towards a complete picture using all of the fossils: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 106, p. 177–192.
- EASTON, W.H., 1960, *Invertebrate Paleontology*: Harper and Row, New York, 701 p.
- ETTENSCHN, F.R., 1994, Tectonic control on formation and cyclicity of major Appalachian unconformities and associated stratigraphic sequences: *in* Dennison, J.M. and Ettensohn, F.R., eds., *Tectonic and Eustatic Controls on Sedimentary Cycles*: Society of Economic Paleontologists and Mineralogists Concepts in Sedimentology and Paleontology, No. 4, p. 217–242.
- ETTENSCHN, F.R., GREB, S.F., CHESNUT, D.R., JR., HARRIS, D.C., MASON, C.E., EBLE, C.F., HOWELL, P.D., WATSON, A.E., and JOHNSON, W.K., 2002, Mississippian stratigraphy, depositional environments, and tectonic framework of the Central Appalachian Basin, eastern Kentucky, U.S.A.: *in* Hills, L.V., Henderson, C.M., and Bamber, E.W., eds., *Carboniferous and Permian of the World*: Canadian Society of Petroleum Geologists Memoir 19, p. 22–40.
- FELL, H.B., 1966, *Ecology of crinoids*: *in* Booloottian, R.A., ed., *Physiology of Echinodermata*: Wiley Interscience, New York, p. 49–62.
- GAHN, F.J., and KAMMER, T.W., 2002, The cladid crinoid *Barycrinus* from the Burlington Limestone (early Osagean) and the phylogenetics of Mississippian botryocrinids: *Journal of Paleontology*, v. 76, p. 123–133.
- HESS, H., AUSICH, W.I., BRETT, C.E., and SIMMS, M.J., 1999, *Fossil Crinoids*: Cambridge University Press, Cambridge, 316 p.
- HARVEY, E.W., and AUSICH, W.I., 1997, Phylogeny of calceocrinid crinoids (Paleozoic: Echinodermata): biogeography and mosaic evolution: *Journal of Paleontology*, v. 71, p. 299–305.
- HOLMDEN, C., CREASER, R.A., MUEHLENBACHS, K., LESLIE, S.A., and BERGSTRÖM, S.M., 1998, Isotopic evidence for geochemical decoupling between ancient epeiric seas and bordering oceans: implications for secular curves: *Geology*, v. 26, p. 567–570.
- ITANO, W.M., WEBSTER, G.D., HOUCK, K.J., and BATEMAN, W.D., 2003, The first Pennsylvanian batocrinid and other new echinoderms from the Minturn Formation of central Colorado: *The Mountain Geologist*, v. 40, p. 83–100.
- JABLONSKI, D., ROY, K., VALENTINE, J. W., PRICE, R.M., and ANDERSON, P.S., 2003, The impact of the pull of the recent on the history of marine diversity: *Science*, v. 300, p. 1133–1135.
- JELL, P.A., 1999, Silurian and Devonian crinoids from central Victoria: *Memoirs of the Queensland Museum*, v. 43,1, p. 1–114.
- JELL, P.A., and JELL, J.S., 1999, Crinoids, a blastoid and a cyclocystoid from the Upper Devonian reef complex of the Canning Basin, Western Australia: *Memoirs of the Queensland Museum*, v. 43,1, p. 201–236.
- JELL, P.A., and THERON, J.N., 1999, Early Devonian echinoderms from South Africa: *Memoirs of the Queensland Museum*, v. 43,1, p. 115–200.
- KAMMER, T.W., 1985, Aerosol filtration theory applied to Mississippian deltaic crinoids: *Journal of Paleontology*, v. 59, p. 551–560.
- KAMMER, T.W., and AUSICH, W.I., 1987, Aerosol suspension feeding and current velocities: distributional controls for late Osagean crinoids: *Paleobiology*, v. 13, p. 379–395.
- KAMMER, T.W., and AUSICH, W.I., 1992, Advanced cladid crinoids from the Middle Mississippian of the east-central United States: primitive-grade calyces: *Journal of Paleontology*, v. 66, p. 461–480.
- KAMMER, T.W., and AUSICH, W.I., 1993, Advanced cladid crinoids from the Middle Mississippian of the east-central United States: intermediate-grade calyces: *Journal of Paleontology*, v. 67, p. 614–639.
- KAMMER, T.W., and AUSICH, W.I., 1994, Advanced cladid crinoids from the Middle Mississippian of the east-central United States: advanced-grade calyces: *Journal of Paleontology*, v. 68, p. 339–351.
- KAMMER, T.W., and AUSICH, W.I., 1996, Primitive cladid crinoids from upper Osagean–lower Meramecian (Mississippian) rocks of east-central United States: *Journal of Paleontology*, v. 70, p. 835–866.
- KAMMER, T.W., BAUMILLER, T.K., and AUSICH, W.I., 1997, Species longevity as a function of niche breadth: evidence from fossil crinoids: *Geology*, v. 25, p. 219–222.
- KAMMER T.W., BAUMILLER, T.K., and AUSICH, W.I., 1998, Evolution-

- ary significance of differential species longevity in Osagean–Meramecian (Mississippian) crinoid clades: *Paleobiology*, v. 24, p. 155–176.
- KAMMER, T.W., and GAHN, F.J., 2003, Primitive cladid crinoids from the early Osagean Burlington Limestone and the phylogenetics of Mississippian species of *Cyathocrinites*: *Journal of Paleontology*, v. 77, p. 121–138.
- KAMMER, T.W., and LAKE A.M., 2001, Salinity ranges of Late Mississippian invertebrates of the central Appalachian basin: *South-eastern Geology*, v. 40, p. 99–116.
- LANE, N.G., 1971, Crinoids and reefs: Proceedings of the North American Paleontological Convention, September 1969, Part J, p. 1430–1443.
- LANE, N.G., 1972, Synecology of Middle Mississippian (Carboniferous) crinoid communities in Indiana: Twenty-fourth International Geological Congress, *Comptes Rendues Section 7*, p. 89–94.
- LANE, N.G., 1984, Predation and survival among inadunate crinoids: *Paleobiology*, v. 10, p. 453–458.
- LANE, N.G., MAPLES, C.G., and WATERS, J.A., 2001a, Revision of Late Devonian (Famennian) and some Early Carboniferous (Tournaisian) crinoids and blastoids from the type Devonian area of North Devon: *Palaeontology*, v. 44, p. 1043–1080.
- LANE, N.G., MAPLES, C.G., and WATERS, J.A., 2001b, Revision of Strunian crinoids and blastoids from Germany: *Palaeontologische Zeitschrift*, v. 75, p. 233–252.
- LANE, N.G., WATERS, J.A., and MAPLES, C.G., 1997, Echinoderm faunas of the Hongguleleng Formation, Late Devonian (Famennian), Xinjiang-Uygur Autonomous Region, People's Republic of China: *The Paleontological Society, Memoir 47*, 43 p.
- LANE, N.G., WATERS, J.A., MAPLES, C.G., MARCUS, S.A. and LIAO, Z.-T., 1996, A camerate-rich Late Carboniferous (Moscovian) crinoid fauna from volcanic conglomerate, Xinjiang, Peoples Republic of China: *Journal of Paleontology*, v. 70, p. 117–128.
- LAUDON, L.R., 1948, Osage–Meramec contact: *Journal of Geology*, v. 56, p. 288–302.
- LEBOLD, J.G., and KAMMER, T.W., 2006, Gradient analysis of faunal distributions associated with rapid transgression and low accommodation space in a Late Pennsylvanian marine embayment: biofacies of the Ames Member (Glenshaw Formation, Conemaugh Group) in the northern Appalachian Basin, U.S.A.: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 231, p. 291–314.
- LEE, K.G., AUSICH, W.I., and KAMMER, T.W., 2005, Crinoids from the Nada Member of the Borden Formation (Lower Mississippian) in eastern Kentucky: *Journal of Paleontology*, v. 79, p. 337–355.
- LEEDER, M.R., 1992, Dinantian: in Duff, P.McL.D., and Smith, A.J., eds., *Geology of England and Wales*: Geological Society, London, p. 207–238.
- LEES, A., and MILLER, J., 1995, Waulsortian banks: Special Publication, International Association of Sedimentologists, v. 23, p. 191–271.
- LEVIN, H.L., 1994, *The Earth Through Time*, 4th edition: Saunders College Publishing, Fort Worth, 651 p.
- LEVIN, H.L., 1996, *The Earth Through Time*, 5th edition: Saunders College Publishing, Fort Worth, 607 p.
- LEVIN, H.L., 1999, *The Earth Through Time*, 6th edition: Saunders College Publishing, Fort Worth, 568 p.
- LOWENSTAM, H.A., 1957, Niagaran reefs in the Great Lakes area: in Ladd, H.S., ed., *Treatise on Marine Ecology and Paleocology*: Geological Society of America Memoir 67, part 2, p. 215–248.
- MACARTHUR, R.H., and WILSON, E.O., 1967, *The Theory of Island Biogeography*: Princeton University Press, Princeton, 203 p.
- MACURDA, D.B., JR., 1973, Ecology of comatulid crinoids at Grand Bahama Island: *Hydro-lab Journal*, Freeport, Bahamas, v. 2, p. 9–24.
- MACURDA, D.B., JR., and MEYER, D.L., 1983, Sea lilies and feather stars: *American Scientist*, v. 71, p. 354–365.
- MATCHEN, D.L., and KAMMER, T.W., 1994, Sequence stratigraphy of the Lower Mississippian Price and Borden formations in southern West Virginia and eastern Kentucky: *Southeastern Geology*, v. 34, p. 25–41.
- MCGHEE, G.R., JR., 1996, *The Late Devonian Mass Extinction*: Columbia University Press, New York, 303 p.
- MCINTOSH, G.C., 2001, Devonian cladid crinoids: families Glossocrinidae Goldring, 1923, and Rutkowskicrinidae new family: *Journal of Paleontology*, v. 75, p. 783–807.
- MEGLITSCH, P.A., 1972, *Invertebrate Zoology*, second edition: Oxford University Press, London, 834 p.
- MEYER, D.L., 1973, Feeding behavior and ecology of shallow-water unstalked crinoids (Echinodermata) in the Caribbean Sea: *Marine Biology*, v. 22, p. 105–129.
- MEYER, D.L., 1997, Reef crinoids as current meters: feeding responses to variable flow: Proceedings of the 8th International Coral Reef Symposium, v. 2, p. 1127–1130.
- MEYER, D.L., 1985, Evolutionary implications of predation on Recent comatulid crinoids from the Great Barrier Reef: *Paleobiology*, v. 11, p. 154–164.
- MEYER, D.L., and MACURDA, D.B., JR., 1977, Adaptive radiation of the comatulid crinoids: *Paleobiology*, v. 3, p. 74–82.
- MEYER, D.L., and MACURDA, D.B., JR., 1980, Ecology and distribution of the shallow-water crinoids of Palau and Guam: *Micronesia*, v. 16, p. 59–99.
- MILLER, A.I., and FOOTE, M., 1996, Calibrating the Ordovician radiation of marine life: implications for Phanerozoic diversity trends: *Paleobiology*, v. 22, p. 304–309.
- MOORE, R.C., and TEICHERT, C., eds., 1978, *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2*: Geological Society of America and University of Kansas, Boulder and Lawrence, 1027 p.
- PATTERSON, W.P., and WALTER, L.M., 1994, Depletion of  $^{13}\text{C}$  in seawater  $\Sigma\text{CO}_2$  on modern carbonate platforms: *Geology*, v. 22, p. 885–888.
- PETERS, S.E., and FOOTE, M., 2001, Biodiversity in the Phanerozoic: a reinterpretation: *Paleobiology*, v. 27, p. 583–601.
- PETERS, S.E., and FOOTE, M., 2002, Determinants of extinction in the fossil record: *Nature*, v. 416, p. 420–424.
- PHELPS, W., DROSER, M., and AUSICH, W.I., 2003, Early Mississippian encrinites, an extreme case of pelmatozoans dominating the carbonate depositional system and an examination of factors controlling their abundance: *Geological Society of America Abstracts with Programs*, v. 35,6, p. 502.
- PROKOP, R.J., 2002, *Ramacrinus robustus* sp. n. (Crinoidea, Inadunata) from the Koneprusy Limestone, Lower Devonian, Barrandian area (Czech Republic): *Casopis Narodniho Muzea, Rada Prirodovedna*, v. 171,1–4, p. 63–64.
- RAUP, D.M., 1976, Species diversity in the Phanerozoic: an interpretation: *Paleobiology*, v. 2, p. 289–297.
- READ, W.A., BROWNE, M.A.E., STEPHENSON, D., and UPTON, B.G.J., 2002, Carboniferous: in Trewin, N.H., ed., *The Geology of Scotland*: The Geological Society, London, p. 251–299.
- RICHARDSON, J.G., and AUSICH, W.I., 2004, Miospore biostratigraphy of the Borden Formation (Osagean; Tournaisian/Visean) of Kentucky and Indiana, U.S.A.: *Palynology*, v. 28, p. 159–174.
- RONOV, A.B., 1978, The Earth's sedimentary shell: *International Geology Review*, v. 24, p. 1313–1363.
- RONOV, A.B., KHAIN, V.E., BALUKHOVSKY, A.N., and SESLAVINSKY, K.B., 1980, Quantitative analysis of Phanerozoic sedimentation: *Sedimentary Geology*, v. 5, p. 311–325.
- SAUNDERS, W.B., and RAMSBOTTOM, W.H.C., 1986, The mid-Carboniferous eustatic event: *Geology*, v. 14, p. 208–212.
- SEPKOSKI, J.J., JR., 2002, A compendium of fossil marine animal genera: *Bulletins of American Paleontology* no. 363, 560 p.
- SIGNOR, P.W., and BRETT, C.E., 1984, The mid-Paleozoic precursor to the Mesozoic marine revolution: *Paleobiology*, v. 10, p. 229–245.
- SIMMS, M.J., and SEVASTOPULO, G.D., 1993, The origin of articulate crinoids: *Palaeontology*, v. 36, p. 91–109.
- SLOSS, L.L., 1963, Sequences in the cratonic interior of North America: *Geological Society of America Bulletin*, v. 74, p. 93–114.
- SLOSS, L.L., 1988, Tectonic evolution of the craton in Phanerozoic time: in Sloss, L.L., ed., *Sedimentary Cover—North American Craton*: U.S.: Geological Society of America, *The Geology of North America*, v. D-2, p. 25–51.
- SMITH, A.B., 2001, Large-scale heterogeneity of the fossil record: implications for Phanerozoic biodiversity studies: *Philosophical Transactions of the Royal Society of London B*, v. 356, p. 351–367.
- SMITH, A. B., GALE, A.S., and MONKS, N.E.A., 2001, Sea-level change and rock-record bias in the Cretaceous: a problem for extinction and biodiversity studies: *Paleobiology*, v. 27, p. 241–253.

- SMITH, A.B., and JEFFREY, C.H., 2000, Changes in the diversity, taxic composition, and life-history patterns of echinoids over the past 145 million years: *in* Culver, S.J., and Rawson, P.F., eds., *Biotic Response to Global Change: the Last 145 Million Years*: Cambridge University Press, Cambridge, p. 181–194.
- SMITH, L.B., JR., and READ, J.F., 2000, Rapid onset of Late Paleozoic glaciation on Gondwana: evidence from Upper Mississippian strata of the Midcontinent, United States: *Geology*, v. 28, p. 279–282.
- SPRINGER, F., 1900, On the presence of pores in the ventral sac in fistulate crinoids: *American Geologist*, v. 26, p. 133–151.
- SPRINGER, F., 1920, *The Crinoidea Flexibilia*: Smithsonian Institution Publication 2501, 486 p.
- SPRINGER, F., 1926, Unusual forms of fossil crinoids: *Proceedings of the United States National Museum*, v. 67, article 9, 137 p.
- STANLEY, S.M., and POWELL, M.G., 2003, Depressed rates of origination and extinction during the late Paleozoic ice age: a new state for the global marine ecosystem: *Geology*, v. 31, p. 877–880.
- UBAGHS, G., 1978, Skeletal morphology of fossil crinoids: *in* Moore, R.C., and Teichert, C., eds., *Treatise on Invertebrate Paleontology, Part T, Echinodermata 2*, v. 1: Geological Society of America and University of Kansas, p. T58–T216.
- VEEVERS, J.J., and POWELL, C.McA., 1987, Late Paleozoic glacial episodes in Gondwanaland reflected in transgressive-regressive depositional sequences in Euramerica: *Geological Society of America Bulletin*, v. 98, p. 475–487.
- WACHSMUTH, C., and SPRINGER, F., 1897, *The North American Crinoidea Camerata*: Harvard College Museum of Comparative Zoology, Memoir 20, 21, 897 p.
- WALKER, L.J., WILKINSON, B.H., and IVANY, L.C., 2002, Continental drift and Phanerozoic carbonate accumulation in shallow-shelf and deep-marine settings: *Journal of Geology*, v. 110, p. 75–87.
- WATERS, J.A., and MAPLES, C.G., 1991, Mississippian pelmatozoan community reorganization: a predation-mediated faunal change: *Paleobiology*, v. 17, p. 400–410.
- WATERS, J.A., MAPLES, C.G., LANE, N.G., MARCUS, S., LIAO, Z.T., LIU, L., HOU, H.F., and WANG, J.X., 2003, A quadrupling of Famennian pelmatozoan richness: new Late Devonian blastoids and crinoids from northwest China: *Journal of Paleontology*, v. 77, p. 922–948.
- WEBB, G.E., 2002, Latest Devonian and Early Carboniferous reefs: depressed reef building after the Middle Paleozoic collapse: *in* Kiessling, W., Flügel, E., and Golonka, J., eds., *Phanerozoic Reef Patterns*: Society of Economic Paleontologists and Mineralogists Special Publication 72, p. 239–269.
- WEBSTER, G.D., 1997, Lower Carboniferous echinoderms from northern Utah and western Wyoming: *Utah Geological Survey Bulletin* 128, *Paleontology Series*, v. 1, p. 1–65.
- WEBSTER, G.D., 2001, Palaeobiogeography of Devonian and Carboniferous crinoid faunas of Gondwana: *Records of the Western Australia Museum* (2000), Supplement no. 58, p. 403–420.
- WEBSTER, G.D., 2003, *Bibliography and Index of Paleozoic Crinoids, Coronates, and Hemistreptocrinoids 1758–1999*: Geological Society of America, Special Paper 363 (on-line) <<http://crinoid.gsaajournals.org/crinoidmod>> [Checked 2-15-06]
- WEBSTER, G.D., HAFLEY, D.J., BLAKE, D.B. and GLASS, A., 1999, Crinoids and stelleroids (Echinodermata) from the Broken Rib Member, Dyer Formation (Late Devonian, Famennian) of the White River Plateau, Colorado: *Journal of Paleontology*, v. 73, p. 461–486.
- WEBSTER, G.D. and JELL, P.A., 1999a, New Carboniferous crinoids from eastern Australia: *Memoirs of the Queensland Museum*, v. 43,1, p. 237–278.
- WEBSTER, G.D., and JELL, P.A., 1999b, New Permian crinoids from Australia: *Memoirs of the Queensland Museum*, v. 43,1, p. 279–339.
- WEBSTER, G.D., MAPLES, C.G., MAWSON, R., and DASTANPOUR, M., 2003, A cladid-dominated Early Mississippian crinoid and conodont fauna from Kerman Province, Iran and revision of the Glosocrinids and Rhenocrinids: *The Paleontological Society Memoir* 60, 35 p.
- WEBSTER, G.D., MAPLES, C.G., SEVASTOPULO, G.D., FREST, T., and WATERS, J.A., 2004, Carboniferous (Visean–Moscovian) echinoderms from the Bechar Basin Area of western Algeria: *Bulletins of American Paleontology*, v. 368, 98 p.
- WILKIE, I.C., 1984, Variable tensility in echinoderm collagenous tissues: a review: *Marine Behavioral Physiology*, v. 11, p. 1–34.
- WINDLEY, B.F., 1984, *The Evolving Continents*, 2<sup>nd</sup> ed.: John Wiley and Sons, New York, 399 p.
- WRIGHT, J., 1950, A monograph of the British Carboniferous Crinoidea, v. 1, pt. 1: Palaeontographical Society, London, p. 1–24.
- WRIGHT, J., 1951a, A monograph of the British Carboniferous Crinoidea, v. 1, pt. 2: Palaeontographical Society, London, p. 25–46.
- WRIGHT, J., 1951b, A monograph of the British Carboniferous Crinoidea, v. 1, pt. 3: Palaeontographical Society, London, p. 47–102.
- WRIGHT, J., 1952, A monograph of the British Carboniferous Crinoidea, v. 1, pt. 4: Palaeontographical Society, London, p. 103–148.
- WRIGHT, J., 1954, A monograph of the British Carboniferous Crinoidea, v. 1, pt. 5: Palaeontographical Society, London, p. 149–190.
- WRIGHT, J., 1955a, A monograph of the British Carboniferous Crinoidea, v. 2, pt. 1: Palaeontographical Society, London, p. 191–254.
- WRIGHT, J., 1955b, A monograph of the British Carboniferous Crinoidea, v. 2, pt. 2: Palaeontographical Society, London, p. 255–272.
- WRIGHT, J., 1956, A monograph of the British Carboniferous Crinoidea, v. 2, pt. 3: Palaeontographical Society, London, p. 273–306.
- WRIGHT, J., 1958, A monograph of the British Carboniferous Crinoidea, v. 2, pt. 4: Palaeontographical Society, London, p. 307–328.
- WRIGHT, J., 1960, A monograph of the British Carboniferous Crinoidea, v. 2, pt. 5: Palaeontographical Society, London, p. 329–347.
- WRIGHT, V.P., CHERNS, L., and HODGES, P., 2003, Missing mollusks; field testing taphonomic loss in the Mesozoic through early large-scale aragonite dissolution: *Geology*, v. 31, p. 211–214.
- WRIGHT, V.P., and FAULKNER, T.J., 1990, Sediment dynamics of Early Carboniferous ramps: a proposal: *Geological Journal*, v. 25, p. 139–144.
- YOUNG, S.A., SALTZMAN, M.R., BERGSTRÖM, S.M., 2005, Upper Ordovician (Mohawkian) carbon isotope  $\delta^{13}\text{C}$  stratigraphy in eastern and central North America: regional expression of a perturbation of the global carbon cycle: *Palaeogeography, Palaeoclimatology, Palaeoecology*, v. 222, p. 53–76.
- ZEILLER, W., 1974, *Tropical Marine Invertebrates of Southern Florida and the Bahama Islands*: John Wiley and Sons, New York, 132 p.

ACCEPTED OCTOBER 6, 2005

