

## THE UTILITY OF ISOLATED CRINOID OSSICLES AND FRAGMENTARY CRINOID REMAINS IN TAPHONOMIC AND PALEOENVIRONMENTAL ANALYSIS: AN EXAMPLE FROM THE UPPER PENNSYLVANIAN OF OKLAHOMA, UNITED STATES

JAMES R. THOMKA,<sup>1\*</sup> DANIEL MOSHER,<sup>2</sup> RONALD D. LEWIS,<sup>3</sup> and ROGER K. PABIAN<sup>4†</sup>

<sup>1</sup>Department of Geology, University of Cincinnati, Cincinnati, Ohio 45221, USA, thomkajr@mail.uc.edu; <sup>2</sup>Department of Biology, Mount Vernon Nazarene University, Mount Vernon, Ohio 43050, USA, dmosher@mvnu.edu; <sup>3</sup>Department of Geology and Geography, Auburn University, Auburn, Alabama 36849, USA, lewisrd@auburn.edu; <sup>4</sup>School of Natural Resources, University of Nebraska, Lincoln, Nebraska 68583, USA, rpabian@unl.edu

### ABSTRACT

The crinoid fossil record is dominated by isolated ossicles, pluricolumnals, arm segments, and other fragmentary remains resulting from postmortem skeletal disarticulation; however, few studies to date have focused on dissociated crinoid elements in taphonomic and/or paleoenvironmental analysis. A diverse, abundant, and taphonomically variable crinoid fauna recovered from a thin mudstone interval within the Upper Pennsylvanian Barnsdall Formation in northeastern Oklahoma presents a unique opportunity to test the value of incomplete crinoid remains in reconstructing paleoenvironmental conditions and understanding taphonomic patterns. Isolated radial plates were identified to the most precise level possible, commonly genus or species, and used to calculate the minimum number of completely disarticulated individuals; this value was then compared to the number of articulated specimens representing that same taxon to determine the proportion of individuals with cups that have undergone disarticulation into separate ossicles. Cladid taxa are shown to be particularly prone to total disarticulation, with disparid microcrinoids and, somewhat surprisingly, flexibles demonstrating more resistance to disarticulation. Genus-level taphonomic trends among cladid taxa indicate that genera with large but thin cup plates, short anal sacs, and arms capable of adopting a trauma posture are less prone to total disarticulation. Analysis of fragmentary crinoid material recovered from disaggregation of bulk mudstone slabs reveals that thin horizons containing abundant articulated crinoid crowns are enriched in skeletal material and encrusted ossicles relative to thicker subjacent and superjacent intervals, providing further evidence that such horizons represent periods of sediment starvation on the distal shelf that were episodically punctuated by storm events.

### INTRODUCTION

Evidence for rapid postmortem disarticulation of the echinoderm skeleton has been extensively documented in both modern and ancient environments (e.g., Schäfer, 1972; Lewis, 1980; Donovan, 1991; Brett et al., 1997; Ausich, 2001, and references therein). Rapid skeletal disarticulation appears to have an especially strong influence on crinoids, whose fossil and subfossil record is dominated by individual ossicles and pluricolumnal segments. Yet, despite the common occurrence and large volume of crinoidal material in post-Cambrian, particularly Paleozoic, fossil-bearing strata, few studies have focused on the taphonomic and/or paleoenvironmental information that can be obtained from analysis of isolated crinoid ossicles and fragmentary remains, such as pluricolumnals and arm segments. Moreover, the majority of taphonomic and paleoenvironmental studies that have centered on disarticulated crinoids

have exclusively analyzed modern or, less commonly, Pleistocene remains (e.g., Meyer and Meyer, 1986; Améziene-Cominardi and Roux, 1987; Lewis and Peebles, 1989; Lewis et al., 1990; de Echols, 1993; Llewellyn and Messing, 1993; Baumiller et al., 1995; for an excellent Mesozoic exception see Hunter and Underwood, 2009).

The relative lack of attention toward fragmentary crinoid remains in Paleozoic deposits is somewhat surprising, as the value of such incomplete material has been recognized as an important, but neglected, area of crinoid research for some time (Moore, 1938; Moore and Jeffords, 1968; Jeffords, 1978; Lane and Webster, 1980; Holterhoff, 1997b). To date, most studies of disarticulated Paleozoic crinoids have been descriptive, rather than interpretive, consisting of taxonomic descriptions of partial cups and, more commonly, columnal morphotypes; in fact, artificial classification schemes, based entirely on isolated columnals and pluricolumnals, have been erected and used for taxonomic and biostratigraphic purposes (e.g., Yeltysheva, 1956, 1959; Stukalina, 1965, 1966; Moore and Jeffords, 1968; Donovan, 1986, 1989, 1995). A major reason for this descriptive emphasis is the difficulty in accurately identifying dissociated crinoid elements to low taxonomic levels without the occurrence of articulated cups or crowns with which isolated plates can be compared. Hence, faunas consisting entirely, or nearly entirely, of disarticulated material have not been extensively utilized in detailed taphonomic, paleoecologic, and paleoenvironmental analyses at least partly because of the inherent difficulties in working with specimens for which no taxonomic affinities can be confidently recognized (but see Brett and Baird, 1986; Brett et al., 1997; Pabian and Rushlau, 2002).

Fortunately, Upper Pennsylvanian mudrock facies of the North American midcontinent provide promising opportunities for testing the utility of isolated crinoid ossicles and fragmentary crinoid remains in taphonomic and paleoecologic studies since crinoidal remains, including both articulated and disarticulated material, are locally plentiful and easily processed. Further, generic diversity is fairly high and many crinoid-bearing units are well-studied in terms of lithofacies relationships, depositional processes, and paleoecological structure (e.g., Holterhoff, 1996, 1997a). More importantly, of the few previous studies utilizing fragmentary Upper Pennsylvanian crinoid remains, nearly all focused entirely on crinoid taxonomy, systematics, and ontogeny (Moore and Jeffords, 1968; Jeffords and Miller, 1968; Lewis and Strimple, 1990; Esquivel-Macias et al., 2000), leaving the value of such fragmentary remains in paleoenvironmental studies, as opposed to paleobiological or biostratigraphic investigations, largely unexplored.

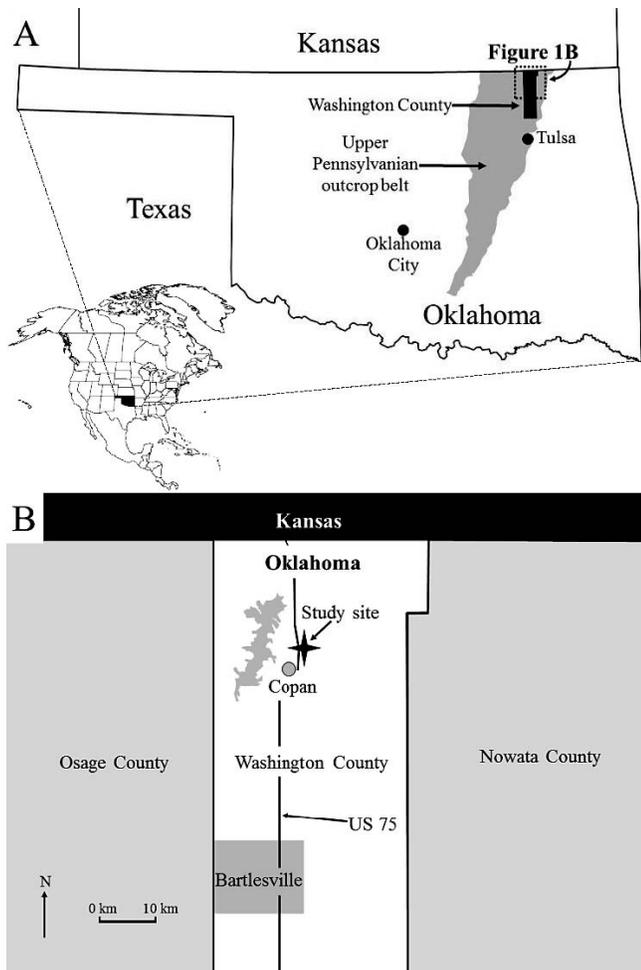
### STRATIGRAPHIC SETTING AND OBJECTIVES

A thin mudstone interval within the middle portion of the upper Missourian Barnsdall Formation, exposed near the small town of Copan, Washington County, northeastern Oklahoma (N36°55'24.58", W95°54'56.61"; Fig. 1), represents a prodeltaic distal shelf environment characterized by slow sedimentation and oxygenated, muddy substrata (Holterhoff, 1997a; Thomka, 2010). To date, 44 crinoid genera and 50

\* Corresponding author.

† Deceased.

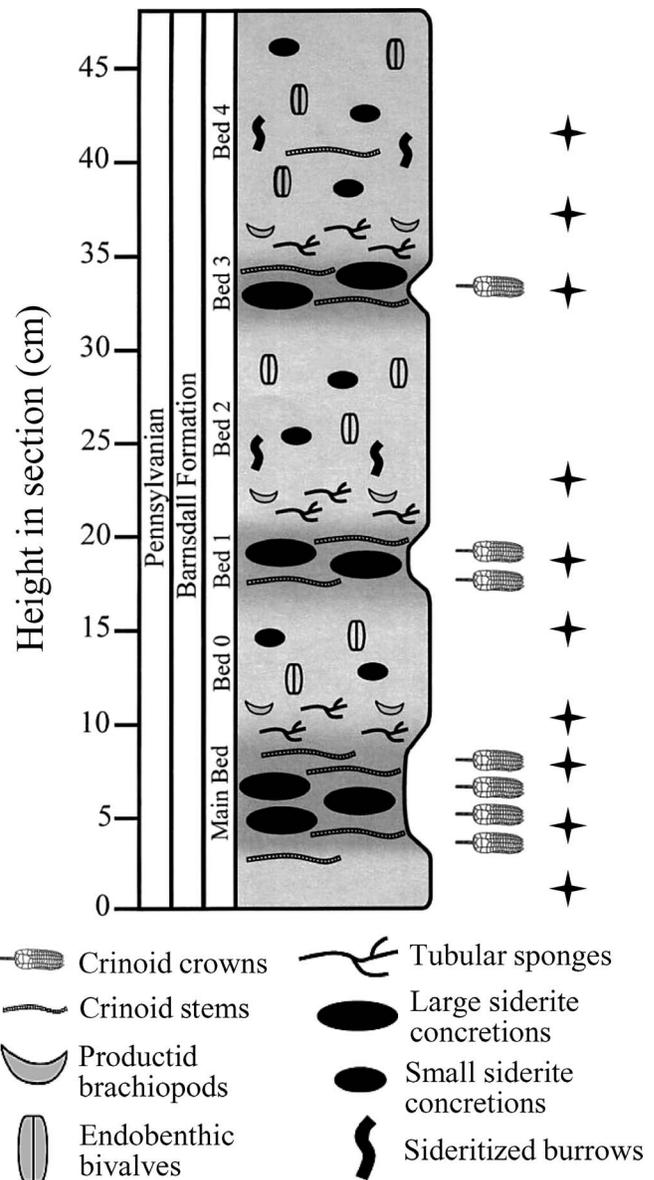
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**FIGURE 1**—Location of study area. A) General setting of Washington County within the Upper Pennsylvanian outcrop belt of Oklahoma. B) Location of study site about 4 km northeast of Copan. To the west of the town is Copan Lake. Modified from Thomka et al. (2011).

species have been recovered from three thin (3–8 cm) horizons within this ~50-cm-thick sequence (Fig. 2), making the Barnsdall Formation host to the highest level of crinoid diversity currently documented within the Pennsylvanian System (Lewis et al., 1998; Thomka et al., 2011). In addition to being exceptionally diverse, much of the crinoid fauna recovered from each thin horizon is remarkably well preserved as a result of episodic tempestitic deposition during periods of shelf sediment starvation. In this setting, the low rates of background sedimentation allowed thin, storm-generated obrution horizons to become stacked, resulting in stratigraphically condensed horizons characterized by taphonomic evidence for considerable exposure of skeletal material at the sediment-water interface, contrastingly associated with evidence for repeated rapid burial by fine-grained sediment (Thomka, 2010).

Articulated crinoid crowns and cups from the Barnsdall Formation have received considerable paleontological attention (Strimple, 1949a, 1949b, 1950, 1951, 1952, 1977; Moore and Strimple, 1969; Thomka et al., 2011), but the abundant isolated crinoid ossicles and pluricolumnals in the matrix sediment have not previously been used as a major data source in investigations into the genesis of the deposit or the comparative taphonomy of the enclosed crinoid specimens. Analysis of fragmentary crinoid remains recovered from the Copan deposit provides enhanced understanding of the paleoenvironmental setting and taphonomy of this unique fauna in three main ways: (1) it makes possible more accurate estimates of species-level rank-abundance by accounting for



**FIGURE 2**—Microstratigraphy of the Copan site showing the occurrence of articulated crinoids at three thin horizons. The stars to the right of the column mark the approximate positions of samples collected for disarticulation. The material used to calculate the proportion of completely disarticulated individuals was collected entirely from the Main Crinoid Bed. Modified from Thomka et al. (2011).

individuals that underwent total disarticulation in between rapid burial events; (2) it allows further recognition of genus-level taphonomic differences between crinoid taxa; and (3) it allows for identification of taphofacies (Speyer and Brett, 1986) and provides evidence for paleoenvironmental processes in a lithologically homogenous section that lacks both bedding planes and physical sedimentary structures as a result of intense bioturbation.

## COMPARATIVE DISARTICULATION

### Materials and Methods

The occurrence of large numbers of articulated cups and crowns alongside isolated radial plates within this deposit allows for reliable family-, genus- or species-level identification of the majority of radial plates by permitting ready comparison between articulated and disarticulated specimens recovered from the same horizon. In a

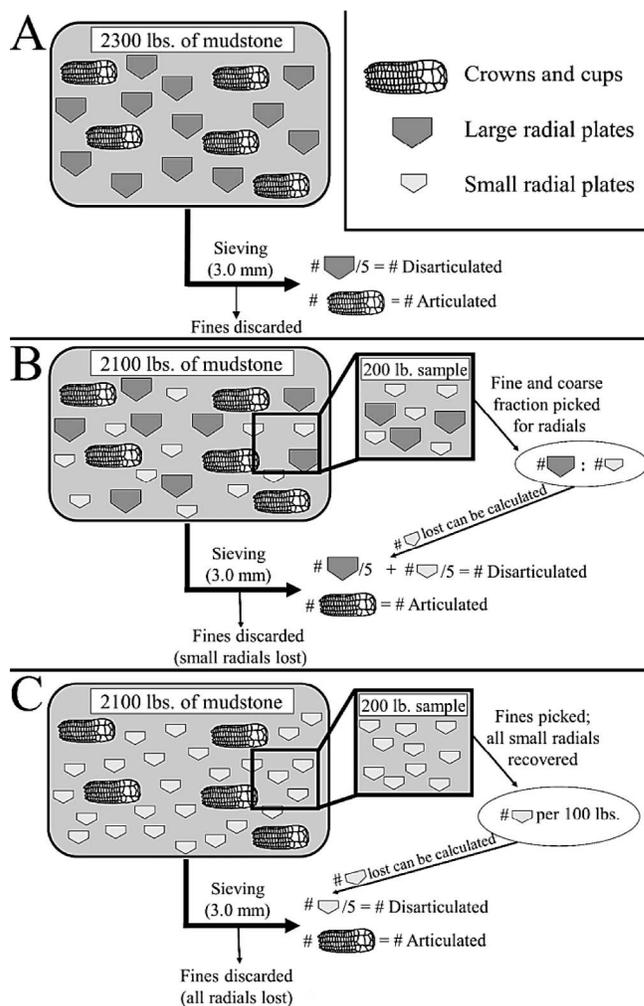
procedure utilized by Lewis (1986) and Holterhoff (1997a) to assess crinoid disarticulation in the Wann Formation and Stanton Formation, respectively, the total number of radial plates for each genus or species was counted and then divided by five to yield the minimum number of completely disarticulated individuals. The ratio of disarticulated to articulated specimens could then be calculated for each genus or species.

The articulated specimens used in this study were collected from the lowest and most prolific of the thin, crinoid-bearing intervals, herein termed the Main Crinoid Bed (Fig. 2). This unit, although only 5–8 cm thick, has thus far yielded over 1200 crinoid cups and crowns, primarily representing advanced cladids (see Thomka et al., 2011). These specimens, which are stored at the University of Nebraska State Museum in Lincoln, Nebraska, were recovered through sieving of bulk mudstone blocks totaling approximately 952 kg (2100 lbs) through a 3 mm screen during a period from 1984 to 1989. This sieved sediment will be referred to as the large sample for the remainder of this report. Although all fossils greater than the 3 mm cutoff, including separate radial plates, were saved during this phase of research, skeletal material less than 3 mm was not. Therefore, any small radial plates or very immature individuals were lost; this makes direct calculation of the proportion of disarticulated individuals based on sieving of bulk mudstone samples (Fig. 3A) accurate only for particularly large crinoid taxa (e.g., *Erisocrinus typus*) whose radial plates would have been retained on the 3 mm screen.

In order to account for the missing data on small taxa, indirect methods of determining the number of radial plates and immature individuals lost during the process of bulk mudstone sieving became necessary. Toward this end, an additional bulk sample weighing 91 kg (200 lbs), herein referred to as the small sample, was collected from the Main Crinoid Bed in 1989 and was picked for all crinoid material greater than 1 mm, found to be the lower size limit of reliable genus- or species-level ossicle identification. For large taxa for which the Direct Method was applicable, the data from the small sample was simply added to the data from the large sample. For other taxa, once the proportion of minute crinoid material in the small sample was determined, the number of radial plates and immature individuals that passed through the 3 mm screen during the main phase of bulk sieving and lost from the large sample could be extrapolated. Two techniques were developed for this extrapolation, termed Indirect Method A and Indirect Method B.

Indirect Method A was necessary for taxa with a considerable size range of radial plates, specifically those for which larger radial plates were retained on the 3 mm screen, and therefore recovered during the main phase of bulk sieving, while smaller radial plates were lost (e.g., *Apographocrinus typicalis*). For these crinoids, the ratio of large to small radial plates was calculated using the 200 lb small sample, and this ratio was then applied to the material recovered during the main phase of bulk sieving, for which the number of large radial plates was known (Fig. 3B). The number of small radial plates lost for each genus could then be estimated and added to the original data.

Indirect Method B was necessary for taxa characterized by small radial plates; for these crinoids, only articulated individuals would have been recovered on the 3 mm screen, while all or the majority of radial plates would have been lost (e.g., *Exocrinus multirami*). The small sample was picked for all radial plates, but since no large radials were recovered from the original phase of bulk sieving, the ratio of large to small radial plates could not be calculated as in Indirect Method A. Instead, the number of radials per unit weight was calculated (radials per 100 lbs.), and this value was then applied to the large sample, for which the total mass of sieved sediment was known (Fig. 3C). This allowed the number of radial plates lost to be calculated, even if few or no radials were recovered during the original phase of bulk sieving. This method was also used to calculate the number of especially tiny articulated or partially articulated individuals recovered during picking of the <3 mm fraction of the small sample.



**FIGURE 3**—Techniques used to calculate the proportion of completely disarticulated individuals. A) Direct Method, used for large taxa with all articulated individuals and all radial plates recovered from sieving at 3 mm. The number of disarticulated individuals (radial plates divided by five) and the number of articulated specimens can be directly compared. B) Indirect Method A, used for taxa of intermediate size. Articulated specimens and larger radials are recovered from sieving at 3 mm, but smaller plates are lost. A 200 lb (91 kg) sample was used to calculate the ratio of large radials to small radials, and this ratio is used to estimate the number of small radial plates that were lost. The total number of large (recovered) and small (estimated) radials divided by five yields the number of disarticulated individuals. C) Indirect Method B, used for small taxa. Only articulated specimens were recovered from sieving at 3 mm and all radials were lost. A 200 lb (91 kg) sample was used to calculate the number of radials per unit weight, and this value is used to estimate the number of radials that were lost. The total number of small (estimated) radials divided by five yields the number of disarticulated individuals.

For many taxa, the proportion of completely disarticulated individuals could be calculated through both indirect methods. Proportions derived from Indirect Method A (as well as the Direct Method) were considered reliable if 40 or more radials were recovered. Proportions derived from Indirect Method B were considered reliable if more than 5 radial plates smaller than 3 mm (i.e., more than one small individual) were recovered from the small sample. When values derived from both indirect estimation techniques were within 0.1 of each other, the average of the two values was considered reliable and used as the proportion of disarticulated individuals for that taxon. These data were used to generate a disarticulation index (DI), defined as the percentage of completely disarticulated individuals. DI values were derived by selecting the most reliable method for calculating the percent of disarticulated individuals (whether determined by counting radials

**TABLE 1**—Proportion of completely disarticulated individuals for selected crinoid taxa. Taxa in bold are common taxa (see text), occurring in great enough numbers to calculate a reliable disarticulation index (DI). The Direct Method, Indirect Method A, Indirect Method B, and Mean columns represent proportions of completely disarticulated individuals; the most reliable values were used to determine DI values, expressed as integers.

	Articulated individuals, large sample	Radial plates, large sample	Articulated individuals >3 mm, small sample	Radial plates >3 mm, small sample	Articulated individuals <3 mm, small sample	Radial plates <3 mm, small sample	Direct method	Indirect method A	Indirect method B	Mean	DI	Notes
<i>Kallimorphocrinus copani</i>	54	7	6	0	20	139			0.525		<b>53</b>	
<i>Lecythiocrinus</i> sp.	6	5	1	0	0	4			0.593			Proportion unreliable: too few radials
<i>Hypselocrinus</i> n. sp.	17	0	1	0	0	3			0.277			Indirect Method B unreliable: too few radials
<i>Elibatocrinus leptocalyx</i>	6	4	1	1	0	2		0.300	0.444	0.372		Proportion unreliable: too few radials
<i>Exoriocrinus</i> sp. cf. <i>E. rugosus</i>	0	21	0	1	0	2						No articulated specimens recovered
<i>Celonocrinus</i> sp.	6	47	1	10	0	9		0.772	0.821	0.797	<b>80</b>	Mean proportion considered reliable
<i>Stellarocrinus virgilensis</i>	30	253	1	13	0	47		0.888	0.839	0.864	<b>86</b>	Mean proportion considered reliable
<i>Clathrocrinus clathratus</i>	5	104	1	11	0	9		0.875	0.879	0.877	<b>88</b>	Mean proportion considered reliable
<i>Erisocrinus typus</i>	58	248	9	24	0	0	0.448					<b>45</b>
<i>Delocrinus subhemisphericus</i>	11	111	0	20	0	1		0.714	0.722	0.718	<b>71</b>	Indirect Method B unreliable: too few small radials
<i>Apographiocrinus typicalis</i>	309	978	36	153	9	562		0.702	0.772	0.737	<b>74</b>	Mean proportion considered reliable
<i>Stenopecrinus planus</i>	17	251	2	13	0	4		0.784	0.765	0.775	<b>78</b>	Indirect Method B unreliable: too few small radials
<i>Triceracrinus</i> sp.	14	23	0	0	0	0	0.247					Direct Method unreliable: juveniles unidentifiable
<b>Undetermined pirasocrinids</b>	25	122	1	13	0	91		0.893	0.901	0.897	<b>90</b>	Mean proportion considered reliable
<i>Galateacrinus ornatus</i>	22	193	0	20	0	163		0.947	0.950	0.949	<b>95</b>	Mean proportion considered reliable
<i>Aesiocrinus detrusus</i>	3	38	0	1	0	0	0.722					Proportion unreliable: too few specimens or radials
<i>Allosocrinus bronaughi</i>	6	112	0	2	0	2		0.884	0.434	0.659	<b>88</b>	Indirect Method B unreliable: too few small radials
<i>Exocrinus multirami</i>	444	0	26	0	4	666			0.748		<b>75</b>	
<i>Euonychocrinus magnus</i>	1	1	0	0	0	0						
<i>Cibolocrinus detectus</i>	8	41	0	4	0	0	0.529				<b>53</b>	
<i>Paramphricrinus oklahomaensis</i>	4 (+9 IBB circlets)	1	0	0	0	0						Possible confusion of radials with brachials
<b>Total</b>	1055	2560	86	286	33	1704						1174 articulated individuals, 4550 radials total

directly, by one of the indirect methods, or by the average of both indirect methods) and multiplying by 100, expressing the result as an integer value.

### Results

The summary data for the proportion of completely disarticulated crinoid taxa are given in Table 1. It is apparent that some taxa are not capable of yielding a DI value due to insufficient numbers of radial plates. For those taxa that are represented by a significant number of

radial plates or more than ten articulated specimens, henceforth referred to as common taxa, DI values were calculated. Thirteen common taxa could be reliably identified to species level based on radial plate morphology, and *Celonocrinus* and *Triceracrinus* radials could be identified to genus. Members of the cladid family Pirasocrinidae could be distinguished from other families, but only *Stenopecrinus planus* and *Triceracrinus* could be identified to genus or species. Unfortunately, the value for *Triceracrinus* is considered unreliable due to problems in identifying the radial plates of juvenile individuals, which were likely included in both the *Triceracrinus* and undifferentiated pirasocrinids

categories. Also, a reliable DI value for *Hypselocrinus* n. sp. could not be calculated due to an insufficient number of radial plates, even though more than ten articulated specimens were recovered.

Three subclasses are represented by common taxa: *Cibolocrinus detectus* represents the Flexibilia, *Kallimorphocrinus copani* represents the Disparida, and the rest of the common taxa belong to the subclass Cladida. Great disparity is observed between noncladids, characterized by low DI values (53 for both flexibles and disparids), and cladids, characterized by DI values, with one exception, exceeding 70.

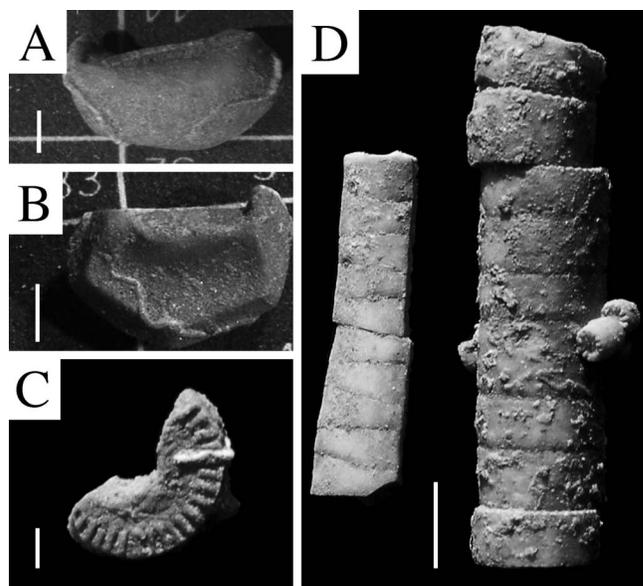
Variation in the relative propensity for total disarticulation is also observed among cladid genera: *Galateocrinus ornatus*, at one extreme, is represented nearly completely (DI = 95) by isolated radial plates, whereas *Erisocrinus typus* is represented primarily by articulated or partially articulated specimens, with disarticulated individuals comprising only 45% of total estimated individuals. Interestingly, this intrasubclass disparity represents the greatest difference in propensity for disarticulation among all crinoid taxa studied, making genus-level variation among taxa within the subclass Cladida greater than subclass-level variation. Yet, even though the proportion of disarticulated individuals belonging to *C. detectus* and *K. copani* falls within the range represented by cladids, it is more likely that *E. typus* and *G. ornatus* represent unique outliers among cladids. In general, the DI values for cladids fall into three groupings: *Delocrinus subhemisphericus*, *Apographeocrinus typicalis*, and *Exocrinus multirami* cluster in the 70–75 range; *Celonocrinus* and *Stenopeocrinus planus* cluster in the 75–80 range; and *Stellarocrinus vigilensis*, *Clathrocrinus clathratus*, pirasocrinids, and *Allosocrinus bronraughi* cluster in the 85–90 range (Table 1).

## TAPHOFACIES ANALYSIS

### Materials and Methods

Numerous mudstone samples, stored at Auburn University and collected from various horizons within the interval shown in Figure 2, were utilized as the source material for analysis of taphonomic and size-distribution trends within the study section. Specifically, samples were collected from (1) immediately below the Main Crinoid Bed, (2) the lower and middle portion of the Main Crinoid Bed, (3) the top of the Main Crinoid Bed, (4) lower Bed 0, (5) upper Bed 0, (6) Bed 1, (7) lower Bed 2, (8) Bed 3, (9) lower Bed 4, and (10) middle Bed 4 (Fig. 2). Individual samples varied in mass and certain intervals yielded more samples than others. This variability reflects complications inherent to collecting from thin, poorly lithified units that were difficult to recognize with certainty in the field and frequently exhibited a pinch-and-swell geometry. Horizons such as Bed 1 and Bed 3 were little more than siderite-rich partings. Collecting large volumes of sediment from such units proved impossible. In contrast, units such as Bed 4 proved considerably easier to collect from, as there was not only more sediment to collect, but individual mudstone blocks tended to remain intact to a greater degree.

Samples were dry-weighed and then immersed in kerosene for a period of one day, which served to break the bonds between flocculated clay minerals. After this period, the kerosene was drained off and an equal volume of water was immediately added, after which the sample was allowed to stand for another day. Allowing the material to remain immersed in water for a longer period resulted in more complete disaggregation. At this point, the samples had become thoroughly disaggregated and consisted of a dense slurry of clastic mud and fossil material. This material was passed through 3.0, 2.0, 1.0, and 0.5 mm sieves, with all fossil material collected, dried, and weighed, providing a weight-based size distribution for skeletal material at each sampled horizon. This approach is utilized in favor of a single minimum-size cutoff due to the possibility of analyzing the size distribution of bioclasts and because of recent studies indicating that the use of several size classes allows for more sensitive assessment of taphonomic data



**FIGURE 4**—Taphonomic features recorded on crinoid ossicles and fragments larger than 2 mm recovered from mudstone disaggregation. A) Exterior surface of *Apographeocrinus typicalis* radial plate with encrusting serpulid-like worm tubes. B) Interior surface of radial plate in A, showing encrustation that could only have occurred after death and disarticulation of the crinoid. C) Columnal exhibiting breakage and encrustation. D) Examples of minor articulation in the form of a pluricolumnal on the right and an arm segment (*A. typicalis*) on the left. Scale bars = 0.5 mm.

(e.g., Kidwell et al., 2001; Kidwell, 2002; Kowalewski and Hoffmeister, 2003; Bush et al., 2007).

The fossil-rich residue for each size class from each sample was picked for crinoid remains using a standard low-magnification binocular microscope. The crinoid fraction of each sample was then weighed to provide information on the relative weight-distribution of crinoidal material. For the >3 mm and 2–3 mm size classes, all crinoid material was identified and categorized as representing either pluricolumnals, columnals, crown plates (brachials, cup plates, and elements of the tegmen), or arm segments. Each ossicle or multiossicle fragment in these size classes was inspected for signs of breakage and encrustation. Arm segments, pluricolumnals, and partial cups were totaled and taphonomically categorized as representing minor articulation. Examples of these taphonomic features are shown in Figure 4.

Fossil material in the 1–2-mm- and 0.5–1-mm size fractions was assessed using a methodology similar to that for the coarser material, although a sample splitter was utilized to create a sample size suitable for microscopic analysis. The crinoid component of these samples was weighed, but underwent no taphonomic analysis or identification, primarily because the small size of individual ossicles impeded identification, and because such minute elements rarely showed encrustation or breakage.

## Results

The results of the bulk mudstone disaggregation, provided in Table 2, indicate that variations in the abundance and taphonomic state of fragmentary crinoid material can be detected between distinct horizons within the studied interval. Figure 5 shows the microstratigraphic distribution of skeletal material and crinoidal material recovered from each of the sampled intervals. It is apparent that relative peaks in skeletal material are present at the Main Crinoid Bed, Bed 1, Bed 3, and middle Bed 4. The highest proportions of crinoidal material are found in Bed 1, Bed 3, Bed 4, and beneath the Main Crinoid Bed. Interestingly, the Main Crinoid Bed itself is represented by a moderate amount of crinoid material. While this may seem surprising, it is likely the result of sampling

**TABLE 2**—Summary of mudstone disaggregation. Pluri = pluricolumnals; Col = columnals; Arm seg = arm segments; CroPl = crown plates; Encr = encrustation; Brk = breakage; Art = minor articulation. Taphonomic features and identity of bioclasts were documented only on crinoid material greater than 2 mm and are given in number of specimens.

	Sample weight (g)	Fossil weight (g)	Fossil density (g / kg)	Crinoid weight (g)	Crinoid density (g / kg)	Pluri	Pluri / kg	Col	Col / kg	Arm seg	Arm seg / kg	CroPl	CroPl / kg	Encr	Encr / kg	Brk	Brk / kg	Art	Art / kg
<b>Middle Bed 4</b>	3901.10	290.63	74.50	62.31	15.97	404	103.56	188	48.19	1	0.26	180	46.14	429	109.97	23	5.90	329	84.34
>3 mm		87.97	22.55	29.96	7.68														
2–3 mm		25.86	6.63	7.71	1.98														
1–2 mm		97.38	24.96	16.96	4.35														
0.5–1 mm		79.42	20.36	7.68	1.97														
<b>Lower Bed 4</b>	4278.51	261.76	61.18	63.80	14.91	241	56.33	117	27.35	17	3.97	319	74.56	455	106.35	40	9.35	258	60.30
>3 mm		59.46	13.90	18.91	4.42														
2–3 mm		27.28	6.38	9.37	2.19														
1–2 mm		77.20	18.04	22.40	5.24														
0.5–1 mm		97.82	22.86	13.12	3.07														
<b>Bed 3</b>	1354.48	113.10	83.50	33.17	24.49	144	106.31	170	125.51	2	1.48	90	66.45	270	199.34	33	24.36	146	107.79
>3 mm		36.67	27.07	12.31	9.09														
2–3 mm		11.73	8.66	5.38	3.97														
1–2 mm		29.70	21.93	10.56	7.80														
0.5–1 mm		35.00	25.84	4.92	3.63														
<b>Lower Bed 2</b>	2221.90	131.95	59.39	14.46	6.51	28	12.60	36	16.20	1	0.45	83	37.36	95	42.76	14	6.30	29	13.05
>3 mm		34.67	15.60	2.54	1.14														
2–3 mm		9.38	4.22	1.68	0.76														
1–2 mm		41.23	18.56	6.40	2.88														
0.5–1 mm		46.67	21.00	3.84	1.73														
<b>Bed 1</b>	831.70	54.07	65.01	19.35	23.27	93	111.82	58	69.74	2	2.40	58	69.74	170	204.40	16	19.24	95	114.22
>3 mm		15.13	18.19	7.30	8.78														
2–3 mm		5.84	7.02	2.93	3.52														
1–2 mm		15.51	18.65	5.92	7.12														
0.5–1 mm		17.59	21.15	3.20	3.85														
<b>Upper Bed 0</b>	466.20	26.64	57.14	4.47	9.59	17	36.47	12	25.74	0	0.00	31	66.50	31	66.50	5	10.73	17	36.47
>3 mm		10.67	22.89	1.61	3.45														
2–3 mm		1.42	3.05	0.54	1.16														
1–2 mm		6.24	13.38	1.44	3.09														
0.5–1 mm		8.31	17.82	0.88	1.89														
<b>Lower Bed 0</b>	6692.28	399.35	59.67	57.95	8.66	194	28.99	172	25.70	12	1.79	207	33.47	358	53.49	41	6.09	206	30.78
>3 mm		109.51	16.36	14.25	2.13														
2–3 mm		35.82	5.35	7.79	1.16														
1–2 mm		133.55	19.96	28.28	4.23														
0.5–1 mm		120.47	18.00	11.36	1.70														
<b>Top of Main Crinoid Bed</b>	1517.35	66.96	44.13	11.01	7.26	30	19.76	28	11.86	35	23.06	76	50.07	66	43.48	9	5.93	65	42.82
>3 mm		21.61	14.24	3.04	2.00														
2–3 mm		4.58	3.02	1.55	1.02														
1–2 mm		18.26	12.03	4.26	2.81														
0.5–1 mm		22.51	14.84	2.16	1.42														
<b>Main Crinoid Bed</b>	3663.69	235.38	64.25	40.28	10.99	200	54.59	129	35.21	10	2.73	224	61.14	327	89.25	47	12.83	210	57.32
>3 mm		63.58	17.35	9.39	2.56														
2–3 mm		32.31	8.82	7.13	1.95														
1–2 mm		59.96	16.37	15.12	4.13														
0.5–1 mm		72.60	18.82	8.64	2.36														
<b>Below Main Crinoid Bed</b>	968.66	39.62	40.90	12.76	13.17	57	58.84	23	23.74	0	0.00	58	59.88	69	71.23	9	9.29	57	58.84
>3 mm		14.38	14.84	4.37	4.51														
2–3 mm		3.18	3.28	1.67	1.72														
1–2 mm		9.60	9.91	4.24	4.38														
0.5–1 mm		12.46	12.86	2.48	2.56														

bias, as blocks containing long lengths of column or articulated crowns were spared from the destructive disaggregation process. The volume of crinoid material previously recovered from the Main Crinoid Bed in the form of articulated specimens and radial plates (see above), although not quantified in terms of weight here, indicates that this interval is actually among the most crinoid rich.

Size distributions (Fig. 6) reveal an absence of consistent dominance by one or two size classes for either total fossil material or crinoidal material, indicating poor sorting. There appears to be no predictable relationship between sampled horizons and the size distribution of its enclosed fossil material, although the 2–3-mm size fraction of fossil material is consistently lower than all other fractions. There is often a

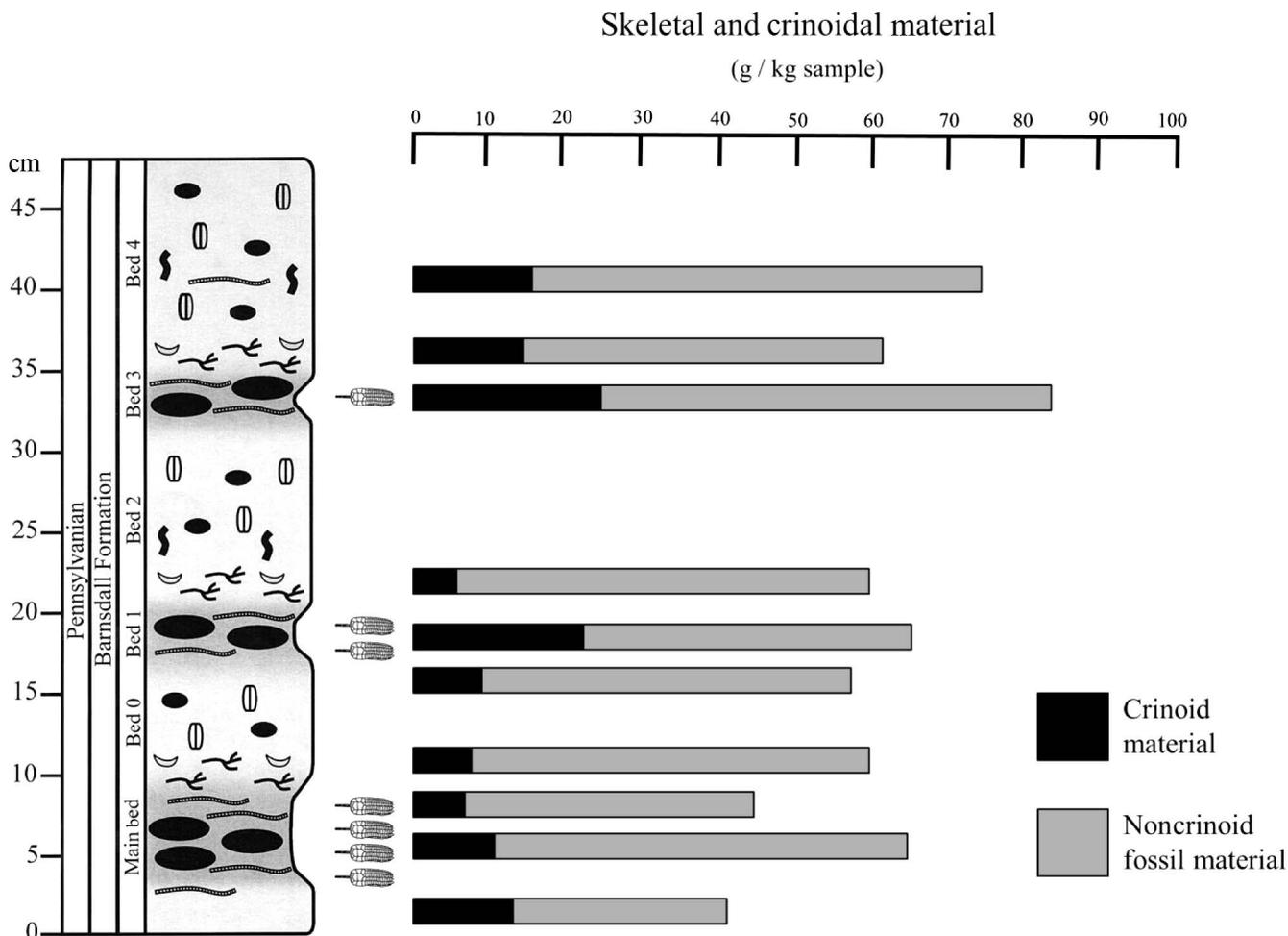


FIGURE 5—Skeletal and crinoidal material at sampled horizons throughout the studied section. Units are grams of fossil material per kilogram of mudstone disaggregated.

poor correspondence between the values of all fossil material and purely crinoidal material for a given size class; that is, a major increase in fossil material in one size fraction does not necessarily result in a similar increase in crinoid material of the same size. In fact, the values for crinoidal material from all size classes are fairly similar to each other, while the corresponding values for all fossil material tend to differ more significantly.

The microstratigraphic distribution of crinoid bioclasts greater than 2 mm, shown in Figure 7, indicates that pluricolumnals and columnals display nearly identical trends, and that these are concentrated in the Main Crinoid Bed, Bed 1, Bed 3, and middle Bed 4. Arm segments are nearly absent in all horizons except for the upper portion of the Main Crinoid Bed, which contains nearly five times as many arm segments as the next richest unit. This peak occurs at the same location as a somewhat unexpected decrease in pluricolumnals, preventing the development of a major peak or drop in crinoid material in the larger size classes. Data on the distribution of crown plates is particularly unusual, as peaks are absent from all three of the thinner units, which typically contain the greatest proportion of crinoid bioclasts. Instead, crown plates are most common below the Main Crinoid Bed, in upper Bed 0, and in lower Bed 2.

The distribution of taphonomic attributes of crinoidal material greater than 2 mm, shown in Figure 8, reveals that encrustation is present throughout the entire section, perhaps due to encrustation prior to death of the crinoids. Nevertheless, pronounced peaks in crinoid bioclast encrustation are present at all three of the thinner units, with the most significant peaks in Bed 1 and Bed 3. Relative lows in encrustation occur in Bed 0 and lower Bed 2. In all sampled horizons,

encrusting epibionts consist overwhelmingly of serpulid-like worm tubes, with bryozoans as uncommon encrusters. Values of breakage were consistently low throughout the section, but minor peaks are present at the thinner units. In general, trends in breakage closely parallel trends in encrustation (Fig. 8). Trends in minor articulation (a metric for the abundance of pluricolumnals, arm segments, and partial cups and anal sacs) also parallel those for encrustation and breakage, with peaks in the thinner units. In this case, however, the Main Crinoid Bed does not stand out strongly and actually has a value slightly lower than that of the underlying horizon. This seemingly reflects the large number of pluricolumnals below the Main Crinoid Bed (Fig. 7). Minor articulation patterns also reflect the enigmatic increase in pluricolumnals through Bed 4, manifest as a relatively steady rise upsection.

## DISCUSSION

### Subclass-Level Taphonomic Variation

Previous taphonomic grade studies (Meyer et al., 1989; Ausich and Sevastopulo, 1994; Taylor and Brett, 1996; Ausich, 2001; Gahn and Baumiller, 2004) have demonstrated a spectrum in relative propensity for total disarticulation among crinoid morphotypes ranging from flexibles, typically the most prone to total disarticulation, to monobathrid camerates, the most resistant to disarticulation. Cladids are slightly more resistant to disarticulation than flexibles but are generally among the most readily disarticulated crinoids, resulting in cladids typically being preserved as either separate ossicles or fairly complete crowns (Brower, 1974; Meyer et al., 1989; Ausich and Sevastopulo,

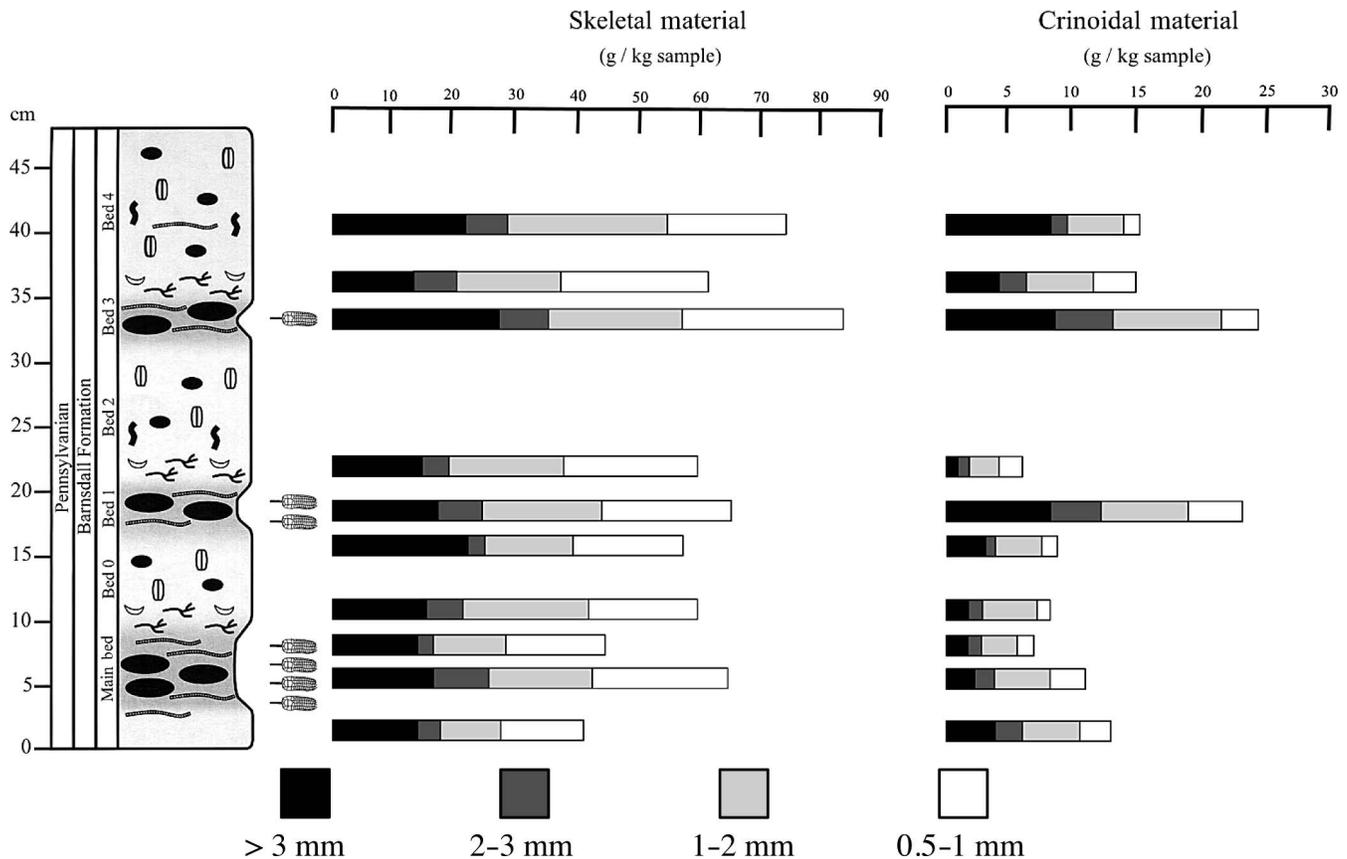


FIGURE 6—Size distribution of skeletal and crinoidal material at sampled horizons throughout the studied section. Units are grams of fossil material per kilogram of mudstone disaggregated. Note the different scales for the graph of skeletal material and crinoid material.

1994; Brett et al., 1997; Ausich, 2001). Disparids tend to be relatively resistant to disarticulation, with microcrinoids representing a particularly robust morphotype (Brett et al., 1997).

Certain results presented here are in agreement with previous taphonomic grade studies that are based predominantly on articulated or partially articulated specimens. Cladid taxa in this study, with the exception of *Erisocrinus typus* (discussed below), are represented primarily by separate radial plates, commonly with only 10%–20% of individuals represented by articulated specimens. This supports the existing taphonomic spectrum of crinoid morphotypes summarized above, in which cladids are particularly prone to total disarticulation. Cladids have been considered as taphonomically equivalent to modern articulate crinoids (Brett et al., 1997; Ausich, 2001), which undergo complete disarticulation under oxygenated conditions within a few hours to a few days after death (Blyth Cain, 1968; Meyer, 1971; Ruhmann, 1971; Liddell, 1975). Morphological factors contributing to the tendency of cladids to undergo rapid and total disarticulation include small cup plates with little connective tissue, absence of interbrachial plates in the calyx, prominent anal sacs that would have been attractive to scavengers and predators (e.g., Lane, 1975, 1984), and long, often biserial and complexly branching arms with muscular connective tissue, which would decay very rapidly and serve as targets of predation and scavenging (Ausich and Baumiller, 1993).

The occurrence of *Kallimorphocrinus copani*, a disparid microcrinoid, in nearly equal numbers of articulated and disarticulated states supports the interpreted robustness of the microcrinoid morphotype. The relative resistance of *K. copani* to disarticulation is likely tied to its small thecal size, which would have minimized predation and scavenging: the amount of viscera within the cup has been shown to be an important control on interpreted scavenging patterns within the Copan cladid fauna (Thomka et al., 2011) and it is logical that this same

relationship is true for other crinoid clades. In addition, microcrinoids are characterized by morphological simplicity, with ligament-bound, monocyclic cups composed of relatively thick plates and unbranched, ligament-bound arms composed of large, thick brachials. The long, thick arm plates would increase resistance to decay due to the small number of junctions and the relatively large amount of connective tissue at each one, and the entirely ligamentary articulations would decrease the likelihood of scavenging and predation on disparids compared to the preferred muscular articulations of cladids (Ausich and Baumiller, 1993). The normal arm position of microcrinoids, with all arms tightly aligned to the long axis of the crown (Sevastopulo, 2008), is analogous to the trauma posture of other crinoids, which appears to be more stable during compaction and may deter scavenging in co-occurring cladids (Thomka et al., 2011). Further, microcrinoids are commonly preserved with a short, rigid proxistele attached to the basal cup cirlet (e.g., Lane and Sevastopulo, 1981, 1982), which may also help to hold the cup plates together.

Interestingly, the flexible morphotype of this fauna demonstrates unexpected resistance to disarticulation, in contrast to previous studies which interpreted flexibles as the most prone to total and rapid disarticulation. In fact, the proportion of totally disarticulated *Cibolocrinus detectus* differs from that of the microcrinoid *K. copani* by less than 5%. Even though the flexibles *Euonychocrinus magnus* and *Paramphicrinus oklahomaensis* have not been recovered in great enough numbers to confidently calculate DI values for these taxa individually (Table 1), genus-level data can be pooled to produce an estimated value for a generalized flexible morphotype. When all taxa are summed, flexibles are represented by 43 radial plates and 22 articulated or partially articulated specimens. This results in a proportion of completely disarticulated flexible individuals of 28.1%, a very low value, well below that for even *C. detectus*. Such a low value may

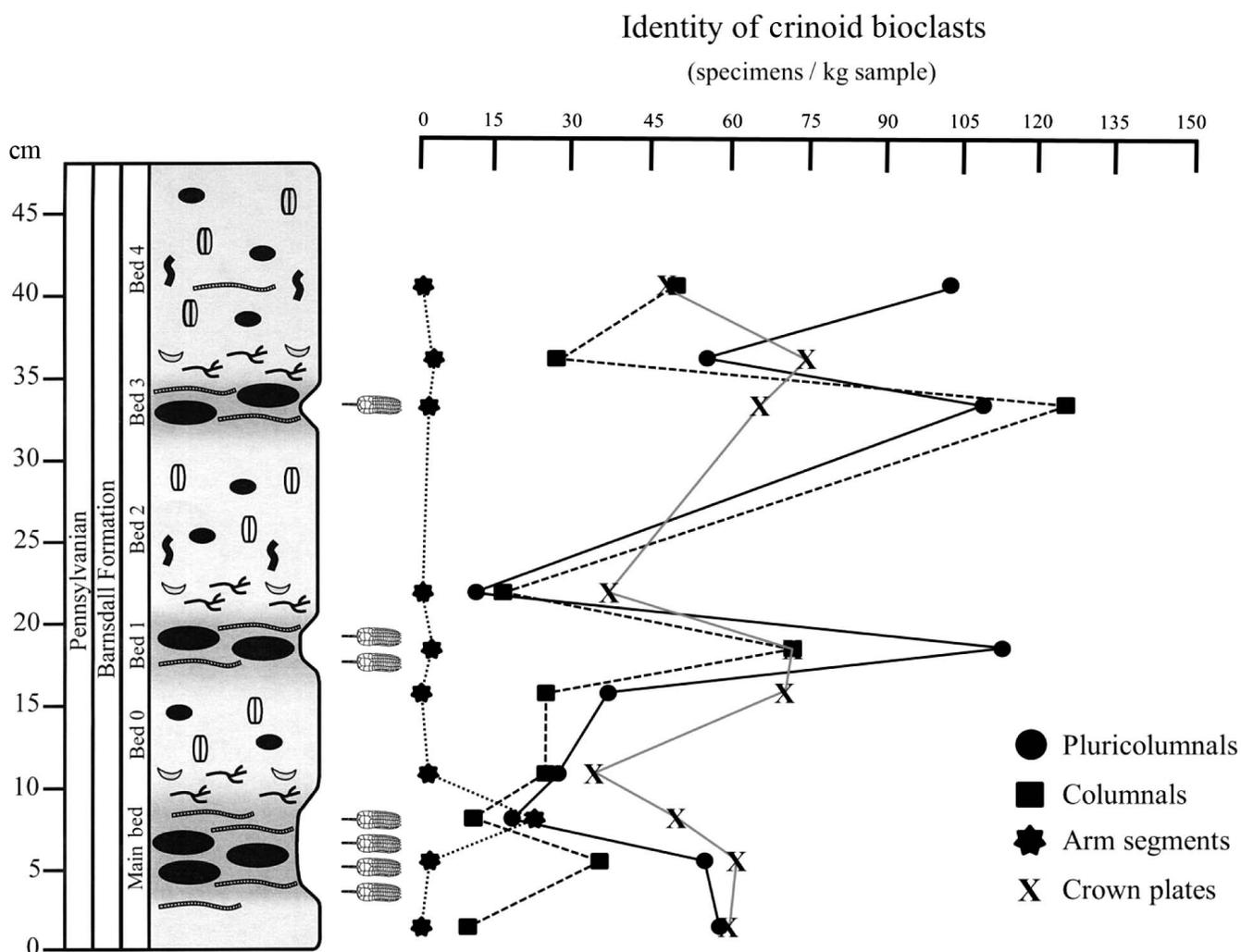


FIGURE 7—Identity of crinoid bioclasts greater than 2 mm at sampled horizons throughout the studied section. Units are number of specimens per kilogram of mudstone disaggregated.

indicate that radial plates of flexibles, with the exception of *C. detectus*, could not consistently be identified or were somehow not recovered, perhaps due to breakage into unidentifiable pieces. Nevertheless, atypically durable flexible taxa have been noted by Ausich (2001), who concluded that certain flexible genera can behave taphonomically comparable to other, more resistant, morphotypes. The exact reasons for this are unclear (Ausich, 2001), although Thomka et al. (2011) found a relationship between the completeness of cladid specimens from the Copan site and the flexibility of their cup: seemingly, taxa with rigid cups rotated slightly during compaction, resulting in a less complete specimen, in contrast to those taxa with flexible cups that were laterally flattened but more complete. It therefore seems likely that the extreme postmortem plasticity of flexible calyxes accounts for the relative resistance to disarticulation in this strongly compacted, fine-grained sediment—flexible individuals, once buried, were easily and severely flattened but were unaffected by later, stronger compaction. Other taxa with less flexible calyxes experienced physical disarticulation resulting from resistance to compactional anisotropy.

#### Genus-Level Taphonomic Variation within Cladids

Thomka et al. (2011) recently studied the taphonomy of articulated and partially articulated cladid specimens from the Copan crinoid fauna, recognizing taphonomic variation manifest in genus-level differences in overall completeness, axis of compaction, arm position,

and indicators of scavenging and decay. These taphonomic attributes were compared between the six most common cladid genera—*Apogrophiocrinus typicalis*, *Exocrinus multirami*, *Erisocrinus typus*, *Stellarocrinus virgilensis*, *Stenopecrinus planus*, and *Galateacrinus ornatus*—allowing the sources of variability to be interpreted. The results of the current study show that taphonomic variation also exists in the relative propensity for total disarticulation among cladid genera (Table 1; Fig. 9) and this permits further elucidation of the causes of intraclade taphonomic variability.

*Erisocrinus typus* (DI = 45) stands out as a taxon that displays unusual resistance to total disarticulation (Fig. 9). Although *Erisocrinus* is among the largest cladids recovered from this deposit, large crown size alone is not a determining factor in contributing to the greater proportion of articulated specimens in this case, as microcrinoids are also resistant to disarticulation (see discussion of *Kallimorphocrinus* above) and because large crowns were most commonly affected by scavenging- or decay-induced disruptions (Thomka et al., 2011). Instead, cup and crown morphology of *Erisocrinus*, specifically the presence of wide and thin cup plates relative to taxa with similarly sized crowns, holds the key to understanding preservation patterns. Thin cup plates resulted in (1) distribution of connective tissue along wide, narrow contacts, prohibiting tight, rigid binding of adjacent cup ossicles during life and (2) increased postmortem fracturing and breakage of ossicles. Consequently, cups responded to strong compaction by breakage of wide plates rather than separation between adjacent

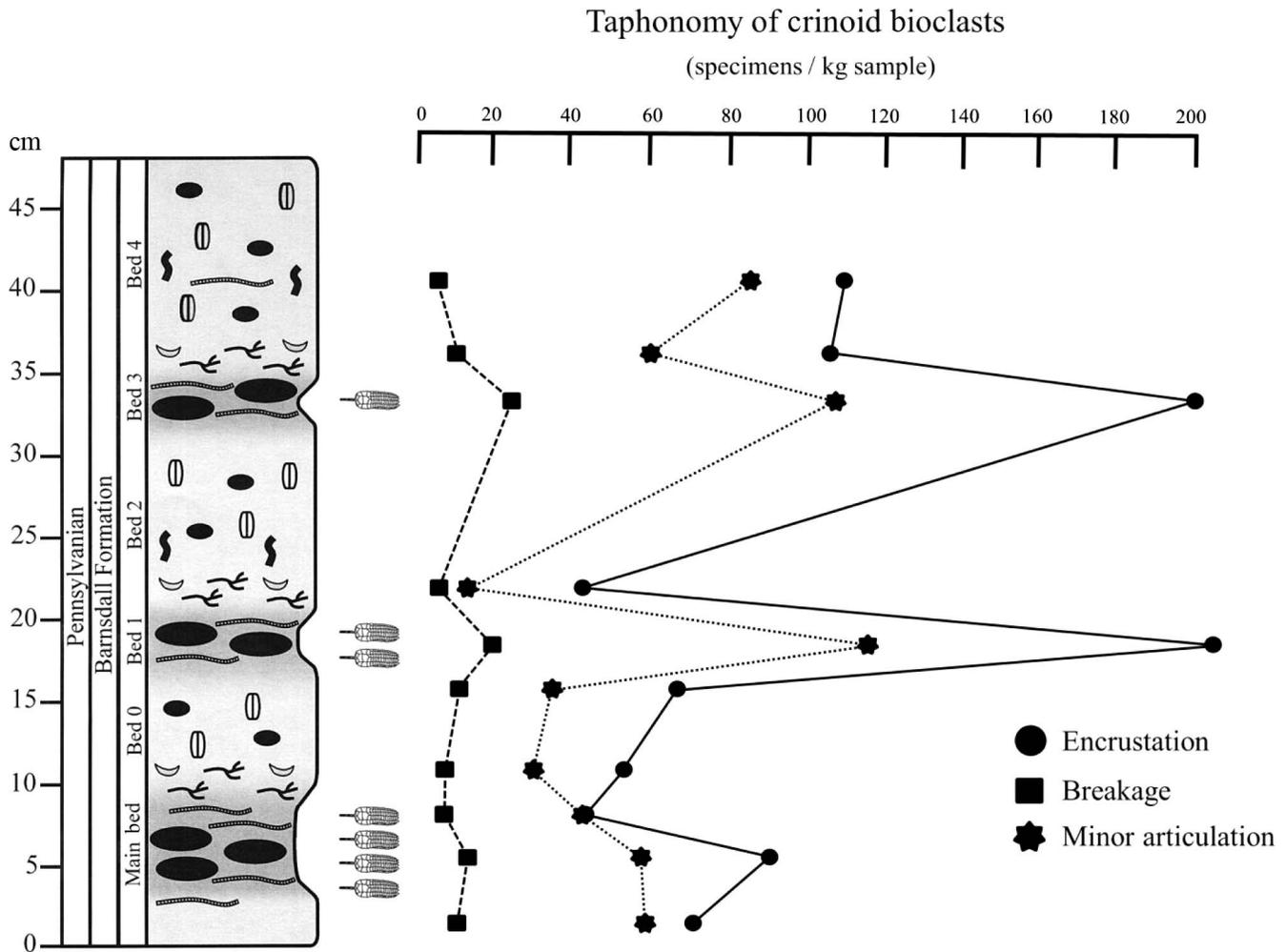


FIGURE 8—Taphonomic features of crinoidal material greater than 2 mm at sampled horizons throughout the studied section. Units are number of specimens per kilogram of mudstone disaggregated. See Figure 4 for examples of these taphonomic attributes.

ossicles and/or by shifting along plate contacts. In general, this increased cup plasticity without increasing plate separation. This response to compaction resembles that of flexible crinoids, which, as discussed above, also have a high proportion of articulated individuals. Additionally, *Erisocrinus* has a simple bowl-shaped cup, wide biserial arms, and a short, stout anal sac. Collectively, these features allow ready adoption of a trauma posture, with all arms aligned parallel to the long axis of the crown and tightly closed; in this case, the entire anal sac would be completely enclosed within the arms. It has been shown that crinoid taxa from this deposit that are commonly found with arms in this configuration tend to be represented by more complete specimens (Thomka et al., 2011). This relationship has been attributed to increased scavenger deterrence and increased stability of buried crowns in this position compared to taxa that could only loosely close their arms, had widely splayed arms, or displayed a prominently protrusive anal sac.

Taxa with mid-range DI values include *Delocrinus subhemisphericus* (DI = 71), *Apogaphiocrinus typicalis* (DI = 74), and *Exocrinus multirami* (DI = 75; Fig. 9). These crinoids also have simple bowl-shaped cups, but composed of thick radial plates relative to cup size, resulting in more rigid cups than those of *Erisocrinus* owing to increased connective tissue between plates and decreased likelihood of plate breakage. *Apogaphiocrinus* is frequently found with its intact cup rotated by compaction but not distorted, whereas the arms, if still attached, are more compressed and offset from the angle of compaction of the cup (Thomka et al., 2011, fig. 13). When disarticulation was

induced by compaction, the boundaries between plates, rather than intraplate planes, were the weakest spots, leading to increased plate separation rather than cup collapse without disarticulation, in contrast to *Erisocrinus*. These genera were capable of adopting a trauma posture that could, like *Erisocrinus*, completely enclose the anal sac, favoring crown preservation; however, these crinoids had relatively few, short, uniserial arms that might not have been able to enclose the tegmen as rapidly or tightly. *Exocrinus* likely has this relatively low value in part because its arms are constructed of tall, robust brachials reminiscent of *Kallimorphocrinus*, discussed above, and because it is the smallest of the cladids studied here (although *Apogaphiocrinus* is typically not much larger). Evidence of postmortem disturbance is restricted only to relatively large specimens of *Apogaphiocrinus* and *Exocrinus* (Thomka et al., 2011), suggesting that these taxa may not have been the first choice of scavengers due both to both fewer arms and less viscera.

Both the families Pirasocrinidae (represented by *Stenopocrinus planus*, DI = 78, and undetermined pirasocrinids, DI = 90) and Stellarocrinidae (represented by *Stellarocrinus virgilensis*, DI = 86, and *Celonocrinus*, DI = 80) have prominent anal sacs incapable of being enclosed by the arms and, rather than simple bowl-shaped cups, have wide, low-profile, often saucer-like cups. The arms of these taxa are generally narrower than those of previously described crinoids; many of these genera are characterized by sticklike uniserial or very narrow biserial arms, suggesting limited flexibility and an inability to adopt a trauma posture. *Stellarocrinus* appears especially limited in terms of possible arm postures due to the high angle of divergence between arms

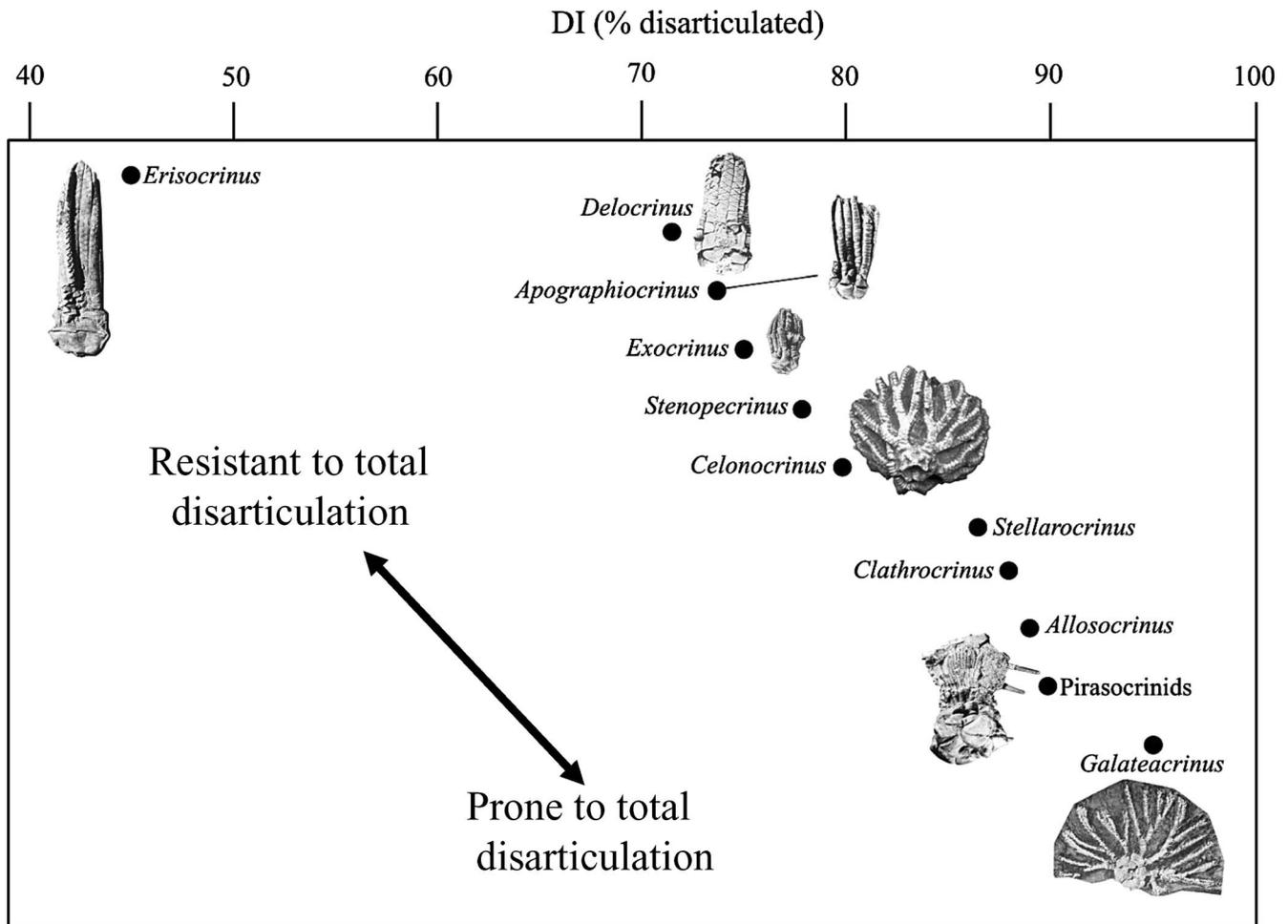


FIGURE 9—Summary of cladid DI values accompanied by photographs of crown morphology for selected genera. Images from Strimple and Moore (1971) and Thomka et al. (2011).

at axillaries. Further, these taxa, particularly pirasocrinids, appear to have been targets of predation during life, as they are well known for their many spinose elements, including spine-bearing axillary brachials and mushroom-shaped anal sacs with platforms bordered by long spines. The large, protruding tegmen structures likely contributed to the higher DI values for these taxa by attracting predators (and scavengers) and possibly preventing crowns from lying flat along the sediment-water interface.

The lower DI value for *Stenopeocrinus* may be related to enhanced cup rigidity relative to other pirasocrinids due to a deeply invaginated infrabasal circler and thicker radial plates. Perhaps more importantly, it has a relatively narrow anal tube, typically with only six spines surrounding the small platform (compared with up to 13 for the pirasocrinid *Polygonocrinus*), which may have allowed this species to be buried at a less unstable angle than other more spinose crinoids. Likewise, the lower DI value for *Celonocrinus* may reflect predator preferences, as this genus has smooth plates and a simpler morphology, lacking the defense mechanisms (i.e., spines) typical of the seemingly predator-preferred stellarocrinids. This may indicate that this genus was not preyed upon as readily as related taxa, perhaps owing to some form of chemical defense (e.g., distasteful compounds within soft tissues).

The high DI values of other taxa can be explained by the morphological features discussed above. *Clathrocrinus* (DI = 88) has a large, robust anal sac and extremely narrow and tall brachials that construct an unusual zigzag structure (cf. Strimple and Moore, 1971, pl. 21) that would have been completely incapable of adopting a trauma posture. *Allosocrinus* (DI = 88) also bears a robust anal sac as well as a low, wide cup. Although this

cup is composed of thin plates, these plates are considerably smaller than those of *Erisocrinus*. The taxon with the highest propensity for complete disarticulation, *Galateacrinus ornatus* (DI = 95), is known as having arms spreading laterally rather than being contracted (trauma posture). The cup is unusual in being nearly flat; its very thick radial plates thin to a narrow facet at the contact with the basals.

In summary, morphologic features conducive to intact preservation include (1) anal sacs that can be completely enclosed within arms, (2) simple bowl-shaped cups, (3) long, wide arms capable of readily adopting the trauma posture, (4) wide, thin cup plates, and (5) an absence of prominent tegmen spines. In contrast, features such as (1) long, prominent, protrusive tegmens, (2) saucer-shaped or low, wide cups, (3) narrow or otherwise inflexible arms, (4) small, thick cup plates, and (5) extreme spinosity are associated with taxa prone to total disarticulation. In general, simple forms appear to be least prone to total disarticulation while more complex or atypical forms display higher DI values. The underlying reasons for this are directly related to stability during burial and compaction, rate of connective tissue decay, and effectiveness of scavenger or predator deterrence. Importantly, in an earlier study of comparative disarticulation based on bulk samples from the shallower and slightly older Wann Formation (Lewis, 1986), *Erisocrinus* was shown to be resistant to disarticulation whereas pirasocrinids disarticulated readily. Thus, propensity for disarticulation appears to be related primarily to the general morphologic and ecologic traits discussed above rather than the specific environmental conditions associated with the Copan deposit.

Studies by Lewis (1986), Allison (1990), and Thomka et al. (2011) have stressed the importance of documenting taphonomic variability

**TABLE 3**—Rank abundance of selected crinoid taxa based on articulated cups and crowns recovered from the phase of bulk mudstone sieving (left) and when completely disarticulated individuals are calculated (right). The minimum number of individuals belonging to each taxon is given in parentheses.

Articulated individuals >3 mm	All articulated and disarticulated individuals
1. <i>Exocrinus multirami</i> (470)	1. <i>Exocrinus multirami</i> (2048)
2. <i>Apographiocrinus typicalis</i> (345)	2. <i>Apographiocrinus typicalis</i> (1706)
3. <i>Erisocrinus typus</i> (67)	3. <i>Kallimorphocrinus copani</i> (612)
4. <i>Kallimorphocrinus copani</i> (60)	4. <i>Galateacrinus ornatus</i> (432)
5. <i>Stellarocrinus virgilensis</i> (31)	5. Undetermined piasocrinids (253)
6. <i>Galateacrinus ornatus</i> (22)	6. <i>Stellarocrinus virgilensis</i> (228)
7. <i>Stenopecrinus planus</i> (19)	7. <i>Erisocrinus typus</i> (122)
8. <i>Hypselocrinus littlecaneyensis</i> (18)	8. <i>Stenopecrinus planus</i> (85)
9. <i>Triceracrinus</i> sp. (14)	9. <i>Allosocrinus bronoughi</i> (52)
Undetermined piasocrinids (14)	10. <i>Clathrocrinus clathratus</i> (49)
11. <i>Paramphricrinus oklahomaensis</i> (13)	11. <i>Clathrocrinus subhemisphericus</i> (39)
12. <i>Delocrinus subhemisphericus</i> (11)	12. <i>Celonocrinus</i> sp. (35)
13. <i>Cibolocrinus detectus</i> (8)	13. <i>Hypselocrinus littlecaneyensis</i> (24)
14. <i>Lecythiocrinus</i> sp. (7)	14. <i>Triceracrinus</i> sp. (19)
<i>Elibatocrinus leptocalyx</i> (7)	15. <i>Lecythiocrinus</i> sp. (18)
<i>Celonocrinus</i> sp. (7)	16. <i>Cibolocrinus detectus</i> (17)
17. <i>Clathrocrinus clathratus</i> (6)	17. <i>Paramphricrinus oklahomaensis</i> (13)
<i>Allosocrinus bronoughi</i> (6)	18. <i>Elibatocrinus leptocalyx</i> (12)
19. <i>Aesiocrinus detrusus</i> (3)	19. <i>Aesiocrinus detrusus</i> (11)
20. <i>Euonychoocrinus magnus</i> (1)	20. <i>Exoriocrinus</i> sp. cf. <i>E. rugosus</i> (9)
21. <i>Exoriocrinus</i> sp. cf. <i>E. rugosus</i> (0)	21. <i>Euonychoocrinus magnus</i> (2)

at low taxonomic levels. Recognition of such taphonomic patterns is critical to interpreting biostratigraphic processes in deposits dominated by a single subclass but diverse at the genus- or species-level. Further, detailed analysis of intraclade taphonomic variation has the potential to reveal historically overlooked, but nevertheless fundamental, controls on crinoid preservation, as biases induced by significant constructional differences are removed and the influence of minor morphological and ecological variations are highlighted. The results of this study provide additional and significant evidence that taphonomic variability extends at least to genus level within advanced cladid crinoids.

#### Reconstructing Biofacies Composition

Although crinoid ossicles are common to overwhelmingly dominant bioclastic components of many Phanerozoic deposits, very few studies have attempted to determine the minimum number of individuals within these facies (see Macurda and Meyer, 1983 for one exception) or calculate rank abundance data for taxa within diverse pelmatozoan assemblages. Because the total number of identifiable ossicles within the Main Crinoid Bed can be extrapolated from the smaller sample, it is possible to derive the number of completely disarticulated individuals; this value can then be added to the number of articulated specimens to calculate the minimum number of individuals belonging to that taxon despite time averaging. Further, calculating the total number of individuals, including both articulated and disarticulated crinoids, results in a more accurate relative abundance ranking for crinoid species and allows for comparison between the ranking based on all individuals and the ranking based solely on articulated specimens. This is important because it highlights taphonomic biases, as the relative abundance of taxa that are prone to total disarticulation will be underestimated and taxa that are resistant to total disarticulation will be overestimated if only articulated specimens are studied.

Table 3 shows a comparison between the relative abundance of crinoid taxa represented only by articulated specimens and the same list when disarticulated individuals are factored in using DI values from Table 1. Both lists are generally similar, with the most common taxa occurring in greater abundance and rare taxa occurring at the bottom of the list regardless of whether or not disarticulated individuals are calculated; however, a number of significant differences can

be recognized. Most notably, the relative resistance to disarticulation characteristic of *Erisocrinus typus* has resulted in it being overestimated relative to other taxa if only articulated specimens were assessed. When the number of disarticulated individuals is counted, *E. typus* drops from the third most abundant taxon to the seventh (Table 3). The same is also true for *Paramphricrinus oklahomaensis*, which dropped from eleventh most abundant to seventeenth and *Hypselocrinus* n. sp., which dropped from eighth most abundant to thirteenth. All of these taxa have low DI values relative to the rest of the taxa evaluated.

In contrast, undifferentiated piasocrinids move from the ninth most abundant taxon to the fifth, above several taxa that had more than double the number of articulated piasocrinid specimens (Table 3). Other taxa showing a similar pattern include *Allosocrinus bronoughi*, moving from seventeenth to ninth, and *Clathrocrinus clathratus*, moving from seventeenth to tenth. All of these taxa are characterized by large DI values (greater than 87; Table 1).

The increase in rank abundance displayed by *Kallimorphocrinus copani* is unusual, as this taxon is resistant to disarticulation and would be expected to experience a drop, rather than a rise, in rank abundance position. The small size of *K. copani*, however, resulted in the loss of many articulated individuals smaller than 3 mm. Seemingly, microcrinoids represent a unique exception to the relationship between resistance to disarticulation and rank abundance described above, as their small size and consequent likelihood of being overlooked (and therefore underestimated) overcompensates for their tendency to remain articulated and otherwise be overestimated.

The minimum number of individuals belonging to each taxon within the sampled area is also given in Table 3. Although the most common taxa are represented by greater numbers of articulated specimens, the calculated minimum number of individuals present after disarticulated individuals are accounted for is considerably greater in most cases; some taxa display increases of an order of magnitude (e.g., *K. copani*, *Galateacrinus ornatus*). In addition, some taxa that appear to be present in similar numbers when only considering cups and crowns become widely separated when disarticulated individuals are factored in (compare *G. ornatus* and *Stenopecrinus planus*; *K. copani* and *E. typus*).

These sorts of quantifications have important implications for paleoecology, as the true composition of paleocommunities (*sensu lato*) may be obscured by taphonomic biases. The crinoid fauna studied here is dominated by a few taxa; however, the identities of the dominant taxa are not necessarily reflected closely by the rank abundance and number of recovered cups and crowns. Consequently, attempts to reconstruct the ecological system represented by the Copan fauna or to define crinoid biofacies for comparative paleoecological studies will be less accurate, or provide less meaningful data, when only the articulated specimens are considered. For example, in a study of crinoid paleoecology of the midcontinent region, Holterhoff (1997a) utilized the Copan fauna to define a unique biofacies characterized by high generic diversity and a large number of ecological guilds; however, nearly all of the taxa occur in assemblages representing separate biofacies as well. Because the presence or absence of diagnostic taxa could not be used as a feature to define a distinctive biofacies, relative abundance became critical: the dominance by *Exocrinus* and *Apographiocrinus* permitted this distinct biofacies to be recognized. Calculation of the total number of individuals, including disarticulated specimens, strongly highlighted the numeric dominance by these two taxa and demonstrated that these were undeniably significant members of this biofacies (Table 3).

#### Taphofacies Analysis and Paleoenvironmental Interpretations

The results of bulk mudstone disaggregation revealed that subtle variations in crinoid abundance and taphonomy can be detected within the 50 cm section under study even though the entire interval is virtually homogeneous lithologically. Thus, two distinct taphofacies, based primarily on isolated crinoid ossicles and fragments, can be identified

within the Copan section. These two taphofacies are associated with the thinner, articulated crinoid-bearing units (Main Crinoid Bed, Bed 1, and Bed 3) and the thicker units lacking articulated crinoids (Bed 0, Bed 2, and Bed 4). Signatures of these two distinct taphofacies are manifest in the relative abundance of skeletal and crinoidal material, relative abundance of certain crinoid bioclasts, and taphonomic attributes of crinoidal material. Although size distribution data do not contribute to the distinction between taphofacies, they do have paleoenvironmental implications and are therefore discussed here.

*Proportion of Skeletal and Crinoidal Material.*—The thinner units are characterized by minor increases in skeletal material and proportion of crinoidal material relative to the thicker units (Fig. 5). This reflects slightly increased stratigraphic condensation of the thinner units associated with periods of sediment starvation of the distal shelf environment. Indeed, further supporting evidence for sediment starvation in the thinner units includes the presence of large siderite concretions and taphonomic and sedimentologic evidence for tempestite deposition of a more distal character than that observed in the thicker units (Thomka, 2010). The thicker units were deposited in a setting characterized by higher sedimentation, creating a dilution effect, and thus decreasing the proportion of fossil material (with the exception of middle Bed 4, discussed further below). The presence of winnowed shell lags and burrowing bivalves preserved in living position within these intervals provide further evidence that the thicker units represent a setting influenced by more energetic storm events with thicker burial layers (Thomka, 2010).

*Size Distribution of Bioclasts.*—Size fraction distribution indicates an absence of bioclast sorting for any of the sampled units; in fact, the >3 mm and 0.5–1 mm classes are often very similar in proportion (Table 2; Fig. 6). The poorly sorted and ungraded nature of this sediment is strong evidence for autochthony or parautochthony of the crinoid fauna, as poorly sorted, ossicle-rich debris has been reported from the living site of recent, offshore, stalked crinoids by Améziane-Cominardi and Roux (1987), Fujita et al. (1987), Messing et al. (1990), and Llewellyn and Messing (1993). This indicates that the Copan deposit bears a sedimentologic signature of autochthony consistent with patterns from modern analogs.

The poor correlation between shifts in the abundance of crinoid material and corresponding shifts in overall fossil material may seem surprising in light of the great volume of crinoidal material recovered from the section. This indicates that shifts in the size distribution of noncrinoid skeletal grains (e.g., large productid brachiopod valves, small fenestrate bryozoan debris) hold greater control over the fossil density and size distribution than do crinoid ossicles for a given horizon.

In a taphonomic field study of sediments deposited during simulated *Acanthaster* outbreaks, Greenstein et al. (1995) reported elevated abundances of asteroid material in the 1–2 mm and 2–4 mm size fractions, but found no increase in material in the largest or smallest fractions, concluding that intermediate size classes were increased at the expense of the largest grains. No similar pattern is observed with the Copan data: it appears that no single size class is a particularly accurate indicator of increases in crinoid abundance here. It seems that the cumulative relative abundance of crinoidal material of all size fractions is the best way to recognize intervals of increased crinoid abundance.

*Identity of Crinoid Bioclasts.*—The microstratigraphic distribution of crinoid bioclast types is related to the character and recognition of taphofacies and provides some insight into the size distributions described above (Fig. 7). Thinner units, particularly Bed 1 and Bed 3, are characterized by increases in both pluricolumnals and columnals. This contrasts with preliminary results presented by Thomka et al. (2010), who reported an increase in pluricolumnals, and a corresponding decrease in columnals, within the thinner units, attributing this disparity to more frequent rapid burial events during deposition of the thinner units and, therefore, increased articulation. Instead, the thinner

units are characterized by major increases in isolated columnal plates, with increases in pluricolumnals of equal or lesser magnitude. The co-occurrence of large numbers of both pluricolumnals and columnals in the thinner units can be explained, in part, by the overall greater abundance of crinoids in the more distal, lower sedimentation setting represented by the thinner units. In addition, the large increases in columnals within the thinner units provides further evidence that these units represent periods of sediment starvation, as pluricolumnals can remain articulated for considerable spans of time before decaying to produce isolated columnals (e.g., Baumiller and Ausich, 1992; Baumiller et al., 1995; Meyer, 1997; Ausich and Baumiller, 1998; Baumiller, 2003). In order to produce a spike in columnals, long periods of slow sedimentation during which columns are allowed to remain unburied and experience complete decay of connective ligamentary tissues are required. The greater number of pluricolumnals relative to columnals supports an increased sedimentation rate, interpreted for the thicker units, as final burial of crinoid columns commonly occurred before complete decay. A particularly high sedimentation rate may account for the strong increase in pluricolumnals throughout Bed 4. Thus, an increase in large pluricolumnals is responsible for the increase in fossil and crinoidal content (and minor articulation, below) in middle Bed 4 that contradicts other relationships between thin and thick units.

Patterns involving arm segments and crown plates are more difficult to interpret within a comparative taphonomic framework. The only recognizable peak in arm segments occurs at the junction between the Main Crinoid Bed and lower Bed 0. Why analogous peaks are absent in Bed 1 and Bed 3 is unclear, but may be due to collection of samples from the lower and middle portions of these thin horizons rather than from the uppermost portion. The Main Crinoid Bed is considerably thicker than Bed 1 and Bed 3, so more precise sampling is possible for this unit and impossible for the thinner, stratigraphically higher units. In any case, the occurrence of this peak at the very top of the Main Crinoid Bed may reflect rapid burial of crinoids shortly before the increase in sedimentation rate typical of overlying Bed 0. Thus, the last rapid burial layer that was deposited during the period otherwise characterized by sediment starvation associated with the Main Crinoid Bed may have been less disturbed, in contrast to earlier event beds, which were affected by later storms. Despite the abundance of pluricolumnals, columnals, and arm segments in the thinner units, crown plates are in greatest abundance in neither the Main Crinoid Bed, Bed 1, nor Bed 3. Moreover, peaks in crown plate abundance do not occur in consistent positions with respect to the thinner units. The reason for this is unclear, but it may reflect the dominance in the thinner units of small crinoid taxa, particularly *Exocrinus multirami*, *Apographiocrinus typicalis*, and *Kallimorphocrinus copani*, whose crowns would disarticulate into ossicles smaller than the 2 mm minimum for identification and counting employed in the disaggregation procedure. Indeed, Figure 6 shows that the 1–2 mm size fraction of crinoidal material increases dramatically from upper Bed 0 to Bed 1 and from Bed 2 to Bed 3. Hence, the crown plate distribution shown in Figure 7 may reflect more uncommon, larger taxa and therefore appear more random.

*Taphonomic Attributes of Crinoid Bioclasts.*—Analysis of taphonomic attributes of ossicles arguably provides the most fruitful data for identifying taphofacies. Large peaks in encrustation are present in the thinner units (Fig. 8), and some ossicles are encrusted on both sides (Figs. 4A–B), indicating a more complex taphonomic history involving overturning of crinoid bioclasts between quiescent intervals that would have been conducive to epibiont growth. This provides strong evidence that these units accumulated over a long period of time in an environment characterized by low turbidity, slow sedimentation rates, and oxygenated conditions (Parsons and Brett, 1991). Furthermore, in an actualistic study of echinoid comparative taphonomy, it was shown that the only taphofacies dominated by encrustation of tests was a sediment-starved marine shelf environment where hard skeletal

material remained in a stable orientation (Nebelsick et al., 1997; Nebelsick, 1999). The relatively low values of encrustation in the thicker units suggest that sedimentation was too high to permit extensive colonization of, and growth on, isolated hard substrates.

Although preferential encrustation of columns over crowns (Feldman and Brett, 1998) and smooth over irregular crinoid bioclast surface textures (Powers and Ausich, 1990; Gluchowski, 2005) have previously been reported, no significant preferences were detected within this deposit, but rigorous quantitative data on these variables were not collected as part of this study. Pabian and Rushlau (2002) report numerous epibionts on both articulated crowns and isolated crown plates of crinoid taxa from strata correlative to the Copan site in comparable shelf environments further to the north. This is consistent with our observations of the Copan crinoid fauna. Seemingly, the occurrence of hard substrata on the otherwise muddy seafloor was more important to encrusters than the nature or identity of the clast being encrusted.

The minor peaks in breakage, present at the thinner units (Fig. 8), may seem at odds with the numerous indicators of these intervals as representing low energy environments. However, ossicle breakage does not necessarily have to result from physical reworking or turbulent events; instead, this may reflect destructive biological processes operating during periods of slow sedimentation. Speyer and Brett (1986) reported increased breakage of Devonian trilobite fragments in fine-grained, low energy facies, inferring greater scavenging of exposed carcasses. Llewellyn and Messing (1993) also interpreted increased breakage of modern crinoidal material in areas of little sediment cover as resulting from more intense scavenging and/or predation. Alternatively, the large amount of fossil material and siderite in the thinner units, when subjected to intense postdepositional compaction, led to increased breakage by contact between skeletal grains and concretions in the subsurface.

The peaks in minor articulation observed in Bed 1 and Bed 3 (Fig. 8) are related to the large numbers of pluricolumnals in these units (Fig. 7). Although there is a peak in arm segments at the top of the Main Crinoid Bed, the number of arm segments (Fig. 7) is insignificant relative to the number of pluricolumnals, so no peak in articulation is present at this horizon (Fig. 8). In spite of the large values for articulation in Bed 1 and Bed 3, minor articulation is not a valuable criterion for characterizing the taphofacies of the thinner units, as these units also contain large numbers of individual columnals (Fig. 7). As mentioned above, the co-occurrence of numerous columnals and pluricolumnals reflects the abundance of columns exhibiting varying degrees of decay, providing further evidence of time averaging in the thinner units.

## CONCLUSIONS

Isolated crinoid ossicles and fragmental crinoid remains such as pluricolumnals and arm segments are common bioclasts in the Upper Pennsylvanian Barnsdall Formation of northeastern Oklahoma, United States, where they occur in matrix sediment associated with a diverse assemblage of articulated crinoid cups and crowns. While these articulated remains have received considerable attention, the disarticulated material had not been utilized as a major source of taphonomic and paleoenvironmental data in previous studies. This is generally the case for deposits containing abundant articulated crinoid specimens.

By comparing the number of articulated specimens of the common genera to the number of disarticulated individuals as represented by isolated radial plates, subclass-level trends between cladids, disparids, and flexibles are recognized. Cladids are prone to total disarticulation, with articulated specimens typically comprising 10%–20% of individuals; disparids and flexibles demonstrate more resistance to disarticulation, with roughly equal numbers of articulated and completely disarticulated individuals. This agrees, for the most part, with previous taphonomic grade studies, wherein cladids tend to be preserved in a disarticulated state, and disparid microcrinoids are particularly robust

morphotypes. Flexibles have historically been viewed as the most prone to disarticulation in previous studies, making the resistance of flexibles to disarticulation in this deposit anomalous. Notable genus-level taphonomic variability is detected within cladids, related to the width and thickness of cup plates, ability to adopt a trauma posture, and anal sac and arm morphology; hence, this study provides further evidence that taphonomic variation extends to low taxonomic levels within advanced cladid crinoids.

The proportion of completely disarticulated individuals belonging to each taxon, when combined with the number of articulated specimens, allows the minimum number of individuals to be calculated. This results in a more accurate estimation of the paleoecological makeup of this fauna than is possible using only articulated crowns and cups, as taxa that are prone to total disarticulation are underestimated while taxa that are resistant to total disarticulation are overestimated.

Isolated ossicles and fragments recovered from disaggregation of mudstone slabs resulted in the recognition of taphonomic properties useful in refining paleoenvironmental interpretations of the horizons containing articulated crinoids. The thin intervals containing abundant articulated crowns are characterized by (1) an increase in skeletal material and crinoid material relative to subjacent and superjacent intervals, (2) an abundance of columnals and pluricolumnals, and (3) an abundance of encrusted and broken crinoid grains. Collectively, these indicate that the Main Crinoid Bed, Bed 1, and Bed 3 are stratigraphically condensed units representing long periods of slow sedimentation and low energy where multiple generations of crinoids lived, died, and disarticulated to differing extents (i.e., pluricolumnals vs. columnals) prior to final burial. Bed 0, Bed 2, and Bed 4 represent environments where sedimentation was sufficient to prevent much encrustation and create a dilution effect, resulting in low values of skeletal and crinoidal material. All horizons within the microstratigraphic section are poorly sorted with regard to both skeletal material and crinoidal material, suggesting autochthony.

Although this study focused on the paleoenvironmental and taphonomic value of crinoid fragments and ossicles at a single site, the types of analyses performed for this research can be easily applied to practically any other crinoid-bearing deposit. More importantly, this study demonstrates that crinoids can serve as sensitive recorders of taphonomic and environmental processes even after undergoing complete skeletal disarticulation. Despite being easily overlooked, crinoid ossicles represent a major data source for comparative taphonomic, paleoecologic, and sedimentologic investigations and should be considered as a promising tool for future research.

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