Disarticulation patterns in Ordovician crinoids: Implications for the evolutionary history of connective tissue in the Crinoidea

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Taphonomic information is examined to evaluate the early history of connective tissues in the Crinoidea. The pattern of stalk segmentation of Middle and Late Ordovician crinoids is consistent with the two-ligament (intercolumnal and through-going ligaments) pattern present in living isocrinid crinoids and interpreted for fossil isocrinids, holocrinids, and Lower Mississippian crinoids. A single rhombiferan was also examined; its taphonomic pattern is also indicative of this style of tissue organization. Furthermore, the taphonomy of all Middle and Late Ordovician crinoids may reflect that they lacked discretely organized muscles between arm brachials, which is consistent with the hypothesis that muscles evolved as a connective tissue between plates only once within the Crinoidea, during the Early Devonian. These data indicate that the two-ligament organization of the stalk is a primitive feature among the Crinoidea and perhaps even among stalked echinoderms. Therefore, the autotomy function of this column-tissue organization among living crinoids is an exaptation. On the other hand, discretely organized muscles as connective tissue in crinoid arms is a derived trait that first appeared during the middle Paleozoic; this adaptation proved very successful for the advanced cladid crinoids. □*Crinoids, taphonomy, evolutionary paleobiology.*

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Multi-element endoskeletons consisting of individual plates of high-magnesium calcite connected to each other by soft tissues provide the structural support for crinoids. Adjacent plates may be bound to each other during life by two types of soft tissues, ligament and muscle, or by cementation. Articulations may consist of one or a combination of these materials. For example, plates can be solely cemented (ankylosed), solely connected with ligamentary tissue, or connected with ligamentary tissue and a slight degree of cementation. Muscular tissue, when present, is always combined with ligamentary tissue in an antagonistic lever system. Functionally, the different articulations offer vastly different possibilities for interplate movement. For example, a cemented articulation cannot move, whereas ligamentary and muscular articulations provide varying degrees and types of movement. The ligamentary tissue of crinoids (Wilkie *et al.* 1993), as of all echinoderms, is highly unusual in that its viscoelastic properties can be actively modified by the organism. Because of this property, the tissue has been referred to as mutable collagenous tissue (MCT; Motokawa 1984; Wilkie 1984). Although MCT cannot be actively contracted (but see Birenheide & Motokawa, 1996) because of its variable tensile properties, it plays an extremely important role in the functional morphology of echinoderms (Wilkie & Emson 1988). For example, it can be modified very rapidly into a stiff, 'catch' state that allows an individual to withstand large external forces passively, such as those of fluid drag, without undergoing large deflections and without expending energy beyond that involved in going into 'catch.' Thus, particular postures may be maintained inexpensively for long periods of time. Despite the versatility of MCT, articulations with this tissue can only respond to external forces; MCT does not possess contractile abilities comparable to muscle (but see Birenheide *et al.* 1994; Birenheide & Motokawa 1996). Thus, the most versatile articulations are those that possess muscles, which are actively contractile, and MCT. These articulations allow rapid movement employing muscles and MCTs in the low-stiffness state, but they also possess the ability to lock into position using the 'catch' mode of the MCT.

Different arrangements of tissues are also functionally significant. For example, living isocrinid stalks are bound by two types of ligamentary tissue, intercolumnar ligaments and through-going ligaments (Grimmer *et al.* 1985). Intercolumnar ligaments are short fibers that penetrate only a short distance into a columnal, thereby only connecting two adjacent columnals. Through-going ligaments are long and penetrate a series of columnals from the proximalmost internodal of a noditaxis to the next nodal distally (all nodals in isocrinids bear cirri). Thus, in the stalks of isocrinids the only articulation lacking through-going ligament is the articulation between a nodal and an infranodal. This articulation has a distinctive morphology called a synostosial articulation. It occurs at regular intervals along the stalk of an isocrinid and is specialized for autotomy, a process that has been documented by laboratory experiments (Wilkie *et al.* 1993; Rosenkrantz & Baumiller 1994) and by *in situ* observations (Baumiller *et al.* 1995).

This study examines relevant data for determining the geological history of connective tissues in the stalk and arms of crinoids utilizing several previously developed taphonomic methods and a new method for analyzing isolated pluricolumnals. The functional significance of connective tissues for crinoid ecology makes consideration of this history important. Are the specialized functions of tissues and tissue arrangements present in living crinoids the result of adaptive change, and if so, when and under what paleoecological conditions did such adaptations occur? Alternatively, are these functions exaptations of previously developed soft-tissue arrangements that had developed for other reasons? Previously, Baumiller & Ausich (1992) and Ausich & Baumiller (1993) interpreted the tissue types among Lower Mississippian crinoids, and in this study we will attempt to extend the temporal knowledge of crinoid connective tissues by consideration of Middle and Late Ordovician crinoids. In addition, three Middle Ordovician rhombiferan specimens are also considered.

Materials

Four Ordovician faunas are examined for specimens displaying preserved taphonomic signatures of connective tissue. These are the Middle Ordovician Table Head Group (Whiterockian) in Newfoundland, Canada (Ausich *et al.* 1998), the Middle Ordovician (Blackriverian and Trentonian) echinoderms from Illinois and Wisconsin reported by Kolata (1975), the Middle Ordovician (Blackriverian) echinoderms from central Tennessee monographed by Guensburg (1984), and Upper Ordovician (Cincinnatian) crinoids from the greater Cincinnati, Ohio, area. Relevant data were available from 61 Middle Ordovician and 82 Late Ordovician specimens, including three rhombiferans. For specimens preserved with stalk, the conditions of the stalk and arms (complete or broken) were noted. If the stalk was in an early phase of disarticulation, so that it was broken into segments but still basically intact, the number of columnals in each segment along the stalk was counted.

Methods

The methods employed here are similar to those used by Baumiller & Ausich (1992) and Ausich & Baumiller (1993). Also, a new method, described below, is proposed to identify tissue organization from isolated pluricolumnals. Methods for analysis of stalk and arm patterns are described in separate sections below. The methods rely on the assumption that under normal conditions of decay, articulations with different connective-tissue types should disarticulate at different rates, whereas articulations bound by the same types of tissues should disarticulate at stochastically constant rates. For example, muscular tissue should decay more rapidly than ligamentary tissue, and the intercolumnal ligaments should decay more rapidly than through-going ligaments (see Baumiller & Ausich 1992 and discussion below for distinction of ligament types). If burial and preservation occurred prior to complete disarticulation, distinctive taphonomic signatures should be preserved among crinoids with different tissues or different tissue arrangements. Therefore, recognition of tissues in fossil crinoids is dependent on cataloging taphonomic patterns of crinoids that have, by chance, been preserved in this 'taphonomic window'.

Connective tissues in the stalk

Methods

The null model. – Crinoid stalks consist of individual elements, the columnals, stacked end-to-end and bound together by soft tissue. Hence, one would expect that, after death, decay would begin to weaken the bonds between adjacent columnals. As individual intercolumnal bonds become too weak to hold adjacent columnals together, the stalk would begin to disarticulate. More and more segments would be generated, each segment consisting of one or more columnals. If no process intervenes to inhibit decay and disarticulation, the end result will be individual columnals. For a single stalk consisting of many (>100) columnals, one would expect that, depending on when the taphonomic process terminates, a particular distribution of segments should be produced, with a complete stalk and a fully disarticulated stalk representing the two end-member situations of no decay and complete decay, respectively.

Between the complete and fully disarticulated states, the stalk would go through a sequence of steps. This sequence will involve increase in the number of segments and, therefore, decrease in the average length of each segment. What interests us here are the types of segmentation patterns that would be expected under the null model, that is under a model where disarticulation occurs at random with respect to position along the stalk. This type of a model, in which each articulation has an equal probability of being segmented, is referred to as the 'broken stick'. Under the assumptions of a broken stick, a statistically predictable pattern of pluricolumnal lengths should be generated that follows a hollow-curve distribution. Any significant deviations from the hollow-curve distribution imply either (1) that the fragmentation process is nonrandom or (2) that the system is not closed and that some sorting of fragments by extrinsic agents, such as currents, has occurred, removing from or added to the sample in a nonrandom fashion. Explanation 1 could involve one of two mechanisms: (a) heterogeneities intrinsic to the stalk such as soft-tissue organization or (b) mechanisms of breakage extrinsic to the stalk that operate in a regular, nonrandom fashion. Explanation 1b implies, for example, that there might exist a mechanical propensity for all slender beams, such as a crinoid stalk, regardless of their intrinsic properties, to break in half. If this was coupled with a greater propensity of longer segments to break, the pattern generated would consist of segments of uniform length, with the characteristic length decreasing with time, yet this pattern would have little to do with the intrinsic properties of the beam. At present, we know of no breakage mechanism operating independently of the internal organization of the beam that would generate a nonrandom pattern; therefore, we will not consider possibility 1b further and will restrict our discussion to possibilities 1a and 2. The goal of this approach, then, is to determine whether a sample of stalk fragments can be distinguished from random and, if so, to identify the underlying cause of nonrandomness.

Pluricolumnals representing a single individual. – When fossil pluricolumnals representing the stalk of a single individual are preserved in such a way that they can be aligned end-to-end in the correct order, thus allowing the reconstruction of the original (pre-break) stalk, a method developed by Baumiller & Ausich (1992) may be used to test for stalk heterogeneity. This technique tests whether the observed pattern exhibits a greater degree of regularity in segment lengths than would be expected under the broken-stick model. The test consists of two steps, first the observed pattern is compared to a set of patterns that are 'perfectly regular', i.e. those with segments of equal 'unit' lengths, to identify that unit length which best fits the observations. Next, using a computer, stalks equal in length to the original stalk are broken under the broken-stick scenario into the same number of segments as the observed stalk. The patterns generated in the computer model are also compared to the 'perfectly regular' patterns; if fewer than 5% of these simulated stalks show equal or greater levels of regularity than the observed stalk, the observed stalk is deemed statistically different from the expectations of the random model.

For example, if an observed stalk consists of five segments of the following lengths, -7-6-21-30-7- (a total of 81 columnals; Fig. 1a), the existence of regularity in the pattern is first explored by comparing it to a 'perfect' pattern that would be produced if all segments were of equal length. The 'measure of fit' between the observed and the 'perfect' patterns is computed by taking the square root of the sum of the squared differences between the two patterns. In Fig. 1A the measures of fit of the observed pattern to eleven perfect patterns having characteristic lengths of 5, 6, 7,...15 columnals are plotted (open circles). Among the perfect patterns, the one that most closely resembles the observed pattern (lowest 'measure of fit') is one with a characteristic length of 7 columnals. We now ask whether the level of similarity between the observed pattern and a perfect signal with a characteristic length of 7 truly represents some inherent organization of the stalk into units of 7 columnals, or whether an equal or greater level of similarity could be produced by chance under the broken-stick expectation. To answer this question, i.e. whether the broken stick can produce comparable levels of regularity, 1000 computer simulations were conducted. For each simulation, an 81 columnal long stalk was broken into 5 segments with breaks occurring randomly at any of the 80 articulations (each articulation had been assigned an equal probability, 1/80, of breakage). The 'measure of fit' between each simulated pattern and each of the 'perfect' patterns was calculated, generating 1000 measure of fit values for each potential length. From these, the best (0.1%), the 10th best (1%), and the 50th best (5%) values of measure of fit were retained effectively representing the 99.9%, 99%, and 95% confidence levels for testing whether the observed pattern could be distinguished from the null, broken-stick, model. In Fig. 1A the observed pattern shows a better fit to a 'perfect' pattern with a characteristic length of 7 columnals than do 95% of the null model simulations. Thus, tentatively, the null model must be rejected for this example.

Pluricolumnals representing multiple individuals. – Testing for deviations from the null model using the above method requires a unique type of preservation. Stalks must be preserved following only partial disarticulation and only minimal displacement of adjacent pluricolumnals relative to one another. Fossils preserved in this way are very rare. On the other hand, fossil pluricolumnals and columnals are commonly exceedingly abundant elements of many Paleozoic deposits. Can such aggregations

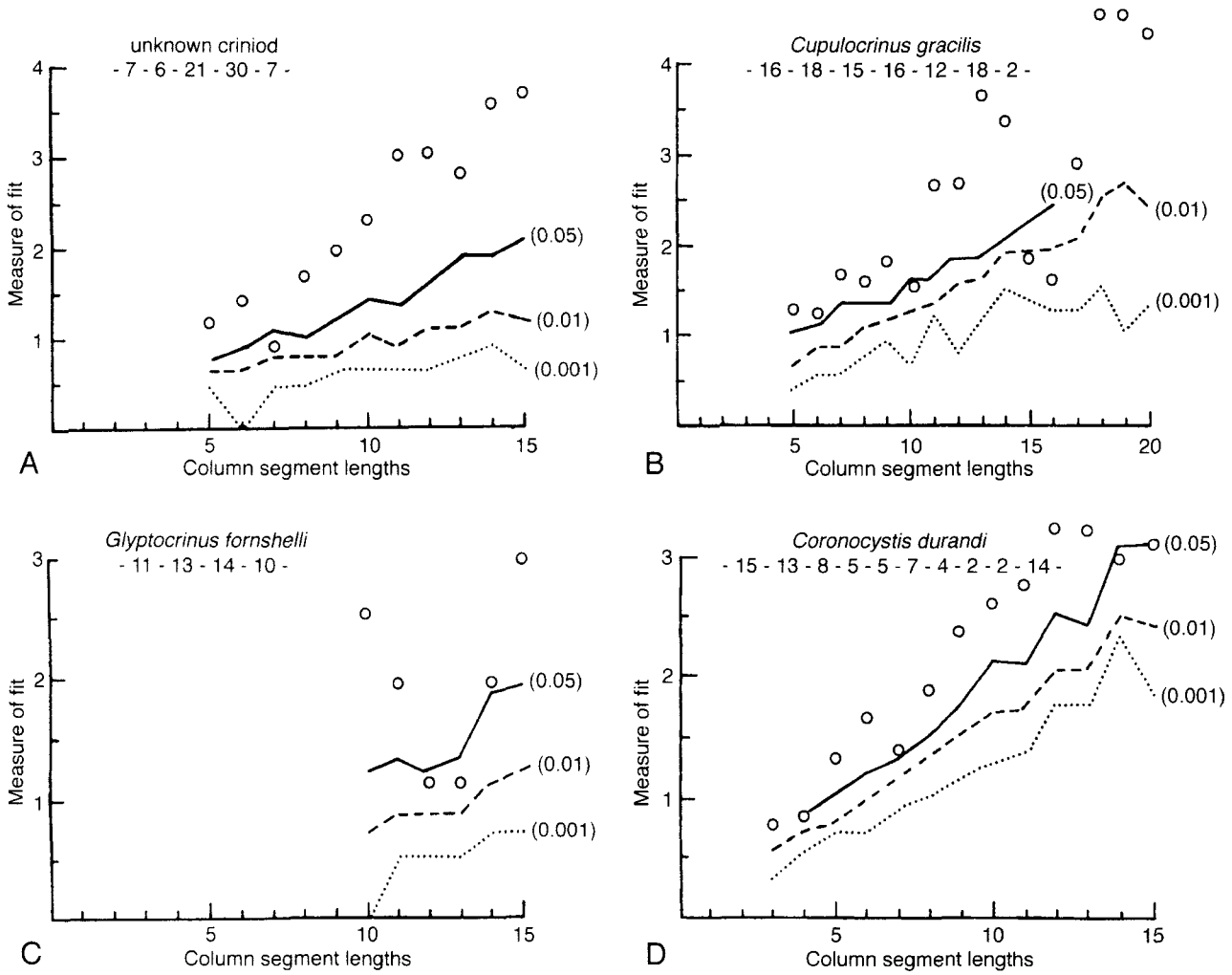

Fig. 1. The measure of fit of (1) the observed data for the stalk of an unknown crinoid consisting of segments of equal length (open circles) and (2) the results of the best (dotted line), the 10th best (dashed line) and the 50th best (solid line) fits of 1000 broken-stick simulations to a perfect pattern consisting of segments of equal length. The fits were calculated for 11 'perfect' patterns with segment lengths of 5, 6,...15 columnals. The measure of fit of the simulations to the perfect patterns was calculated for integer values of segment lengths of 5, 6, ...15 columnals; the lines connecting these data points were constructed for ease of visualization. □A. Five-segment length of an isolated stalk from an unknown Middle Ordovician crinoid. □B. Middle Ordovician *Cupulocrinus gracilis*. □C. Late Ordovician *Glyptocrinus fornshelli*. □D. Middle Ordovician rhombiferan *Coronocystis durandi*. See Tables 1 and 2.

of stalk elements prove useful in reconstructing the distribution of soft tissues? The method outlined here is an attempt to use the distribution of pluricolumnal lengths to test for heterogeneity of soft tissues. This method will be most powerful when evaluating isolated pluricolumnals from a single species.

Based on the sequence of random, broken-stick, disarticulation events described above, what is the predictable random pattern expected from the partial decay of stalks? The expected pattern will vary depending on the number of disarticulation events that have occurred, which is proportional to (1) the total number of columnals in the stalk, N_0, and (2) the time elapsed, t. The distribution of segments of different lengths at time t, ordered from shortest to longest, can be obtained by using the following expression modified from Quinn (1987):

$$L_{i,t} = \frac{N_0}{S_t} \sum_{j=1}^{i} \frac{1}{S_t - j + 1} \qquad 1$$

where L_i is the length of the i-th shortest segment at time t, N_0 is the total length of the stalk expressed as the number of columnals, and S_t is the number of segments the stalk has disarticulated into by time t.

Equation 1 can be used to examine a sample of stalk fragments, such as those of the modern isocrinid *Chladocrinus decorus* that were decayed under laboratory conditions for varying intervals of time. The remains represent the stalks of 13 individuals that were decayed under a vari-

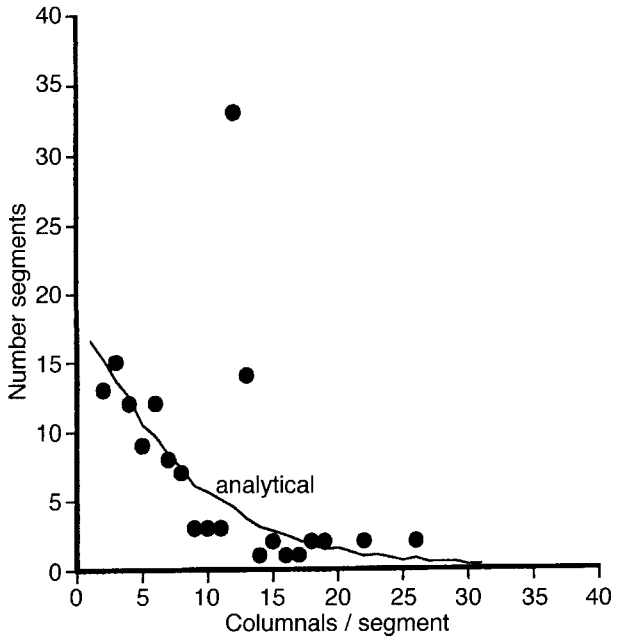

Fig. 2. Distribution of segment lengths from decay experiments conducted on 13 individuals of *Chladocrinus decorus*. The solid line represents the solution of Equation 1 for the data. Note the high number of 12- and 13- columnal-long segments.

ety of conditions and for varying lengths of time. All segments were pooled into a single data set. As Fig. 2 shows, to a first approximation the distribution of fragment lengths follows the predicted 'hollow curve' distribution, although not perfectly. Several points fall off the predicted line, with the 12 and 13 columnal-long fragments seemingly most anomalous. Should the discrepancy between the observed and expected distribution be interpreted as nonrandom, or is it simply the expected noise of a random process? For any given decaying stalk, a range of distributions may be generated under the null model, and the analytical solution represents only the most likely distribution. Thus, the discrepancy may be insignificant: the pattern may be statistically consistent with the null model.

Computer simulations. – To determine how much variability may be generated under the null model, the process of decay can be simulated by computer and repeated many times to generate a range of distributions. This approach allows for confidence intervals to be placed on the analytical solution and, thus, to distinguish statistically nonrandom from random patterns. In each computer simulation a 'stalk' of N_0 columnals was broken into S_t segments, and the distribution of segment lengths was obtained. The process was repeated 1000 times, and the fifth highest, twenty-fifth highest, fifth lowest, and twenty-fifth lowest numbers of segments of each length were obtained. These values correspond to the highest and lowest 0.99, and 0.95 confidence intervals on the expected (average) distribution. Also, we may test whether the simulation process is random by comparing the average distribution of all simulations to the analytical solution; if the simulated process is random, the two should not differ from each other.

The simulation results (Fig. 3) indicate that the computer model does a good job of generating a broken-stick distribution: the average of all simulations is virtually indistinguishable from the analytical solution. However, the results suggest that the distribution of the 12- and 13-columnal segment lengths in *Chladocrinus decorus* is nonrandom and significantly ($P<0.01$) overrepresented. Why the deviation from randomness? As explained in the introduction, isocrinids possess autotomy planes (synostosial articulations) arranged regularly along their stalks that represent planes of taphonomic weakness. In *C. decorus* these planes are generally separated by 12 or 13 columnals, and thus, the 12- and 13-columnal-long segments are more common than expected from a random process operating on a homogeneous stalk.

In the *C. decorus* example above, one of the underlying assumptions of the model, namely that the data represent a single individual, was clearly violated. The effect of having more than a single individual represented in the sample generally should not affect the model's ability to distinguish nonrandom from random patterns. If more than

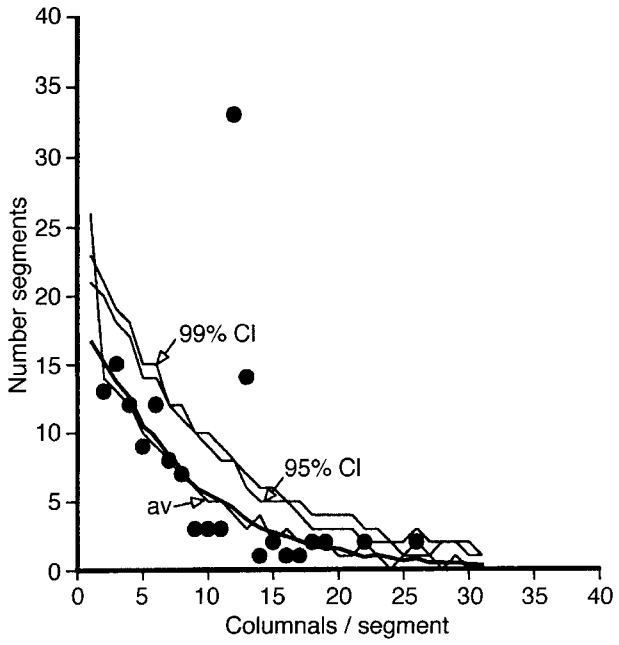

Fig. 3. Distribution of segment lengths of *Chladocrinus decorus* as in Fig. 2. The line labeled 'av.' represents the average distribution of columnal lengths obtained from 1000 simulations of the broken-stick model. The unlabeled line represents the analytical solution (see Fig. 2). The lines labeled '99% CI' and '95% CI' represent the upper 99% and 95% envelopes for the distribution of segment lengths generated by 1000 simulations. The lower envelopes were not included for clarity.

a single individual is represented, there are two important cases to consider: (1) the time of initiation of decay is the same for all individuals and (2) stalks begin disarticulating at different times. If decay is initiated at the same time for all individuals, as would occur following a mass mortality event, the analytical expression and the computer simulations can still be used because the only error introduced will result from the fact that the initial number of segments, S_0, will be underestimated, i.e. the model assumes that all columnals represent only a single individual and that $S_0=1$. Because in the majority of crinoids the number of columnals/individual is high (>100), the underestimate should not be significant. Even this error can be eliminated by estimating the number of individuals in the sample, approximated by dividing the total number of columnals by the number of columnals per individual.

A scenario more realistic than a mass mortality is one where the remains of individuals continue to accumulate as old individuals die, and their stalks are added to the sample. Such a sample will consist of segments of many individuals in different states of fragmentation, some nearly complete, others in partial states of disarticulation, and many fully disarticulated. The fully disarticulated individuals (i.e. those represented by many single columnals) will begin to dominate as the sample ages, whereas all other size classes should reach an equilibrium if the supply of new stalks remains constant through time. Because fully disarticulated stalks are uninformative with regard to the randomness/nonrandomness of the pattern and because their inclusion in the simulation can easily overwhelm the computer's memory and significantly increase the time required to complete each simulation, it would be best to ignore them. However, eliminating part of the sample makes it impossible to apply the described techniques for calculating the initial number of columnals, N_0, and the number of segments, S_i; and without these values, the above computer-modeling approach cannot be applied. To overcome this problem the analytical solution may be invoked, as will be demonstrated below.

As discussed above, given a stalk with a known number of articulations broken into a known number of segments, the distribution of segments of different lengths that is generated under the null model can be predicted using equation 1. The prediction is a statistical one; specifically, it predicts the average distribution. Nevertheless, this expected distribution is unique; it differs from distributions generated by the null model with a different number of segments or with a different number of articulations. For a complete sample, the number of articulations and segments is obtained directly by counting them. If the sample is incomplete (if a category of segment sizes is missing or is not considered, such as, for example, segments of length one) the remaining partial distribution may still be used to reconstruct the complete distribution. This can be done by comparing the observed partial distribution to distributions generated under the null model for a range of values of articulation segment numbers. Using this brute-force approach, the broken-stick distribution that most closely matches the observed partial distribution can be identified. From this predicted distribution, the number of articulations and the number of segments is obtained, and this can then be used in testing for the presence of anomalous frequencies of particular segment lengths in the sample.

It must be noted that in this new approach it is initially assumed that the observed sample was generated under the null, broken-stick model, only to test this assumption later. This may appear to invalidate the method. However, the initial assumption used to approximate the necessary parameters (articulation and segment number) results in values that are conservative in that they will reduce the probability of rejecting the null, random model. The advantages of the above method are that it can accommodate samples that are incomplete (those that lack a certain category of segment lengths). Such a situation may be common in nature, as hydraulic sorting may cause the sample to lose or gain certain sized columnals. Typically, we would expect that a hydraulic process would affect sizes at one tail of the distribution; thus, if it can be shown that one of the tails of the distribution is either over- or underrepresented, the cause may be sorting rather than differentiation of the stalk. Also, the method can be used to study museum samples that may be biased, for example by collectors who concentrated on only longer segments. In this case, the entire small-sized tail of the distribution may be missing, but the sample can still be tested.

Model test. – As was shown above for *Chladocrinus decorus*, the method is capable of identifying patterns that deviate from randomness. It is possible, however, that the method is overly sensitive to such deviations and that it identifies truly random patterns as nonrandom. One way to guard against this would be to set a very conservative level of statistical significance, say $P<0.001$, for nonrandomness. Nevertheless, the application of the method to a crinoid known to lack specialized autotomy planes in the stalk and thus expected to disarticulate under the broken-stick model, would prove a good test of the method's sensitivity. The pluricolumnal remains of one such crinoid, *Apiocrinites*, are readily available. This Jurassic millericrinid lacked the autotomy articulations of isocrinids. When tested with the above method, the observed pattern of segment lengths could not be distinguished from random (Fig. 4). Therefore, as expected, the method implies that the articulations of *Apiocrinites* are undifferentiated with respect to both hard parts and soft tissues.

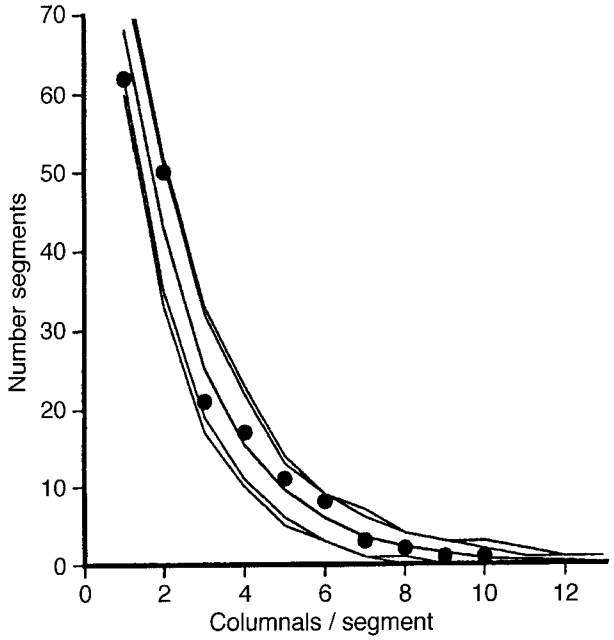

Fig. 4. Distribution of segment lengths of the Jurassic crinoid *Apiocrinus* sp. The middle line represents the average distribution of columnal lengths obtained from 1000 simulations of the broken-stick model. The top two lines represent the maximum 99% (topmost) and 95% envelopes for the distribution of segment lengths generated by 1000 simulations. The two bottom lines represent the minimum 99% (bottommost) and 95% envelopes for the distribution of segment lengths generated by the 1000 simulations.

Results

Ordovician crinoids. – Pluricolumnals of 18 Ordovician stalked echinoderms were analyzed for patterns of segmentation. Each specimen was selected such that there was little doubt that multi-columnal segments represented the stalk of a single individual (see Baumiller & Ausich 1992). Included are seven diplobathrids, four cladids, three disparids, one monobathrid, one rhombiferan, and two column segments not associated with a crown (Tables 1–3).

The patterns exhibited by these pluricolumnals are not as regular as either the Lower Mississippian or the isocrinid examples previously documented (Baumiller & Ausich 1992; Baumiller *et al.* 1995). However, in nearly all cases, observed specimens exhibit a pattern of segment lengths that is nonrandom at the 95% level and, in many cases, at the 99% level. The results of four examples are illustrated graphically as described above. A stalk of unknown affinity with segment lengths of -7-6-21-30-7 columnals shows a nonrandom pattern with a characteristic 'unit' length of 7 columnals at the 95% level (Fig. 1A). For *Cupulocrinus gracilis* (Fig. 1B), fewer than 1% of the simulations produced a pattern as regular as that observed, suggesting characteristic unit lengths of 15 and 16 columnals (10 is also nonrandom in the simulation, but no observed segments are of this length). For *Glyptocrinus fornshelli* fewer than 5% of the 1000 broken-stick simulations generated a pattern of equal regularity; a characteristic length of 12 or 13 columnals provides the best fit to the data. The nonrandom segment lengths for all examined specimens are listed in Tables 1–3 for the 95%, 99%, and 99.9% levels.

As most patterns indicate, most stalks had not broken into the smallest unit-length segments prior to fossilization. For example, in the stalk analyzed in Fig. 1A, not all segments approach the 7 columnal unit in length; several segments have lengths that are integer multiples of the characteristic length ($21=3\times7$; $30\approx4\times7$). For some specimens, the nonrandom unit lengths identified may themselves be integer multiples of the 'true' characteristic unit length. For example, the characteristic unit lengths identified for *Cupulocrinus gracilis* (10, 15, 16, Fig. 1B) may be integer multiples of a true unit length (5 columnals).

Stalk segmentation patterns were also examined by applying the less stringent method to an Upper Ordovician sample of pluricolumnals collected from a single locality. The collection is composed of columnals and pluricolumnals from several specimens of *Cincinnaticrinus* sp. from a small area of a single bedding horizon. The size distribution of 1288 columnals and pluricolumnals (Fig. 5) was analyzed as discussed above. Regardless of whether one includes single columnals in the analysis, the number of 10-columnal-long stalk segments is greater than expected from a broken-stick process at the 99% level of significance.

The Ordovician crinoids examined represent a variety of stalk types, but none are organized into the isocrinid-like, cirri-bearing nodals with a distal synostosis and internodals. None possess specialized skeletally differentiated articulations. However, our results suggest that these Ordovician stalks initially disarticulated into a nonrandom pattern of segments. This holds for examples of all Ordovician clades examined, including monobathrid camerates, diplobathrid camerates, disparids, and cladids. As always, more data would be useful, but the preservational patterns of these Ordovician stalks are consistent with those of isocrinids and Lower Mississippian crinoids (Baumiller & Ausich 1992). The pattern of breakage is not as regular in these Ordovician crinoids as it is in isocrinids with distinct serial repetition of skeletal morphology along the stalk. Given no observable skeletal differentiation, some form of soft-tissue differentiation comparable to isocrinids, with short intercolumnal ligaments between adjacent columnals and long, through-going ligaments penetrating a unit of characteristic length, is a likely explanation for these Ordovician patterns. Most Paleozoic crinoids are characterized by heteromorphic growth of the stalk, where nodals are added beneath the aboral cup and internodals are added sequentially along the stalk,

Table 1. Subdivisions of partially broken stalks and significant stalk-segment lengths among the Middle Ordovician crinoids and rhombiferans described by Kolata (1975) and Guensburg (1984). Number indicates the columnals per segment; Cr, crown; Th, theca; -, at start or end of series indicates stalk end broken; (+), more than number given.

Species	Columnal pattern	Highest significance levels of segment lengths 0.05	0.01	0.001
Diplobathrids				
Reteocrinus polki	Cr-84-35-16-115(+)-	–	16	–
Reteocrinus spinosus	Cr-4-5-6-3-	3	–	–
Reteocrinus variabilicaulis	Cr-20-4-7-10-3-	4	–	–
Rhaphanocrinus buckleyi	Cr-12-1-7-10-	8,9	9	–
Cladids				
Cupulocrinus gracilis	Cr-10-9-18-11-24-4-6-15-	–	–	–
Cupulocrinus gracilis	Cr-16-18-15-16-12-18-2-	10	15,16	–
?Merocrinus britonensis	-10-10-25- and -5-6-5,	6	5	–
Rhombiferan				
Coronocystis durandi	Th-15-13-8-5-3-7-4-2-2-14-	4,14,15	–	–
Unknown	-7-6-21-30-7-	7	–	–

Table 2. Subdivisions of partially broken stalks and significant stalk-segment lengths among the Late Ordovician crinoids from the greater Cincinnati, Ohio, area. Number indicates the columnals per segment; Cr, crown; - , at start or end of series indicates stalk end broken; (+), more than number given.

Species	Columnal pattern	Highest significance levels of segment lengths 0.05	0.01	0.001
Disparids				
Iocrinus subcrassus	-25-21-22-21 40-59-28-20-27	21	21	–
Ectenocrinus grandis	30+-7-7-9-8-18+	8	8	8
Cincinnaticrinus sp.	-11-12-13-10-6-8-9-9-25+	6,8	–	–
Cladids				
Cupulocrinus polydactylus	Cr-14-5-8-6?-6-7-5-10-5-8-10	-	–	–
Monobathrids				
Glyptocrinus fornshelli	-11-13-14-10-	12,13	–	–
Unknown	-7-6-21-30-7-	7	–	–

Table 3. Subdivisions of partially broken stalks and significant stalk-segment lengths among the Whiterockian *Trichinocrinus terranovicus* from Western Newfoundland, Canada (Ausich *et al.* 1998). Number indicates the columns per segment.

Specimen	Column pattern	Highest significance levels of segment lengths 0.05	0.01	0.001
GSC 115971	-8-14-11-?-8-11-	–	–	–
GSC 115961	-9-15-5-7-9-14-	7	–	–
	6-14-9-9-8-1-8-9	8	–	–

although typically only camerates have morphologically distinct nodals. Perhaps it is this method of stalk growth that is responsible for the nonrandom pattern and for serial repetition of through-going ligaments.

The single rhombiferan cystoid studied, *Coronocystis durandi*, also has a nonrandom pattern of segments (Table 1) that is consistent with the same style of ligament organization. In this case, the proxistele is broken into two segments, 15 and 13 columnals each; and the mesistele has a pattern that may represent approximately 4-columnal segments (Fig. 1D, Table 1).

Connective tissues in the arms

Methods

Among living crinoids, muscular connective tissue occurs only on the arms, and this interplate muscular connection is interpreted to have evolved only once, among the pinnulate advanced cladid crinoids during the Early Devonian (Moore & Laudon 1943; Van Sant 1964, pp. 40, 67; Ubaghs 1978; Ausich & Baumiller 1993). Consequently, all other crinoids are thought to have lacked articulations

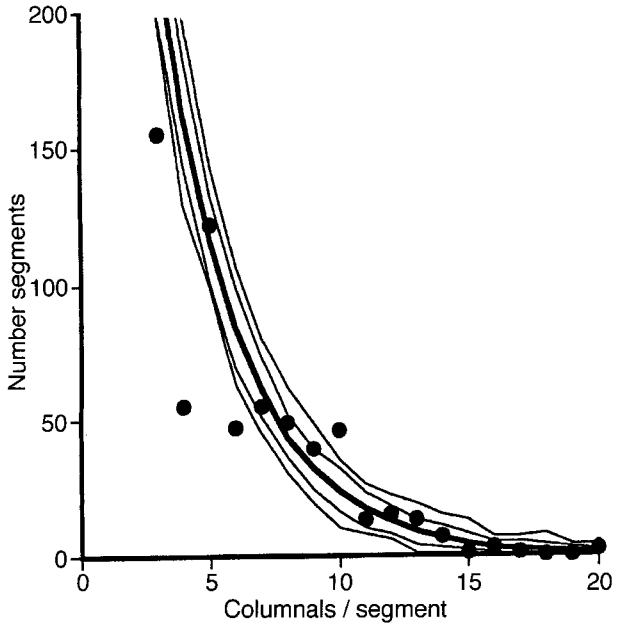

Fig. 5. Distribution of segment lengths of the Ordovician crinoid *Cincinnaticrinus* sp. The middle line represents the average distribution of columnal lengths obtained from 1000 simulations of the broken-stick model. The top two lines represent the maximum 99% (topmost) and 95% envelopes for the distribution of segment lengths generated by 1000 simulations. The two bottom lines represent the minimum 99% (bottom-most) and 95% envelopes for the distribution of segment lengths generated by the 1000 simulations.

with well-differentiated muscular and ligamentary fields between brachials. Traditionally, tests of this interpretation involved considering the morphology and stereomic microstructure of the articular facets. Muscular articular facets are recognized by having a well-developed, central ridge that acts as the fulcrum for the antagonistic action of muscles, on one side, and ligaments, on the opposite side. The microstructure of stereom associated with muscle can also generally be distinguished from that associated with ligament.

An additional test of this interpretation was presented by Ausich & Baumiller (1993), who assumed that different taphonomic patterns would result from the disarticulation of crinoids with muscular arms versus those lacking muscles. The argument is based on the idea that muscle is less resistant to decay than ligament, and thus, structures bound by muscle should segment prior to those bound by ligament. Given that stalk articulations are entirely ligamentary, in taxa with muscular arms the following decay sequence should *generally* obtain (1) completely articulated skeleton, (2) articulated stalk and disarticulated arms, (3) disarticulated stalk and disarticulated arms. In taxa with ligamentary arms, the arms and stalk are taphonomically equivalent and, thus, although states 1 and 3 remain the same as for taxa with muscles, state 2 may be either (a) articulated stalk and disarticulated arms or (b) disarticulated stalk and articulated arms (it is assumed that disarticulation at exactly the same instant is unlikely). Based on this model, Ausich & Baumiller (1993) predicted that the normalized frequency of specimens preserved in state 2b (disarticulated stalk and articulated arms) should be significantly lower for taxa with muscular arms than those with ligamentary arms.

Results

Lower Mississippian crinoids. – By examining specimens in different states of disarticulation among Lower Mississippian crinoids, Ausich & Baumiller (1993) found that the normalized frequency of state 2b among advanced cladids was significantly lower than among all other taxa. This is a result consistent with the interpretation that these crinoids had different arms (muscular) than other taxa (ligamentary).

Ordovician crinoids. – According to traditional interpretations, all of the Ordovician crinoids considered here should have had only ligamentary connective tissues in the arms. Therefore, using the reasoning of Ausich & Baumiller (1993), it is predicted that the arms of all Ordovician crinoids should predictably disarticulate at approximately the same time as the stalk, that stage 2b should be moderately frequent, and that the taphonomic patterns among different taxa should be statistically indistinguishable.

Tables 4–6 are summaries of data gathered on Middle and Late Ordovician crinoids. The most diagnostic test considers the relative proportions of specimens in states 2a and 2b. If large differences in the relative proportions of the two states exist between taxa, that would hint at morphological differences between them; if the proportion of state 2a is much higher than of state 2b, that would imply muscles; if states 2a and 2b occur in roughly equal proportions, that would imply muscleless arms. Although the data for these two states are sparse, the two states occur with equal frequency, and no differences between taxa are apparent. This argues for similar, ligamentary, connective tissue in the arms of all groups.

Another approach for testing for taphonomic differences between taxa is to examine statistically the distribution of all four states in pairwise comparisons. A contingency table was used to evaluate these differences; where data allowed a comparison, no significant differences were found between any pairs of taxa examined (Table 7). Finally, for a crinoid with muscles in the arms, if the arms are broken and brachials are close to their original positions, the stalk should be complete (state 2a), reflecting the differential decay rates. Alternatively, if both arms and column contained only ligaments and disarticulated at approximately the same time, both could be expected to

Table 4. Disarticulation relationships between arms and stalk among the Middle Ordovician crinoids and rhombiferans described by Kolata (1975) and Guensburg (1984). The numbers, 1, 2a, 2b, 3, represent preservational state.

Group	Arms complete		Arms broken	
	Stalk complete *1*	Stalk broken *2a*	Stalk complete *2b*	Stalk broken 3
Diplobathrids	4	1	2	5
Monobathrids	0	0	0	1
Disparids	8	0	1	6
Cladids	3	1	1	7
Hybocrinids	0	0	0	2
Rhombiferans	0	0	0	3
Total	15	2	4	24
Percentages	33%	4%	9%	53%

Table 5. Disarticulation relationships between arms and stalk among Upper Ordovician crinoids from the greater Cincinnati, Ohio, area. The numbers, 1, 2a, 2b, 3, represent preservational state.

Group	Arms complete		Arms broken	
	Stalk complete 1	Stalk broken 2a	Stalk complete 2b	Stalk broken 3
Monobathrids	8	0	1	5
Disparids	23	4	5	16
Cladids	9	2	2	7
Total	40	6	8	28
Percentages	49%	7%	10%	34%

Table 6. Disarticulation relationships between arms and stalk among specimens of crinoids from Western Newfoundland, Canada (Ausich *et al.* 1998). Only specimens with preserved column greater than one-half crown height are counted. The numbers, 1, 2a, 2b, 3, represent preservational state.

Species	Arms complete		Arms broken	
	Stalk complete 1	Stalk broken 2a	Stalk complete 2b	Stalk broken 3
Trichinocrinus terranovicus	2	6	0	4
Isotomocrinus n.sp.	0	2	0	0

be disarticulated but more or less in place (state 3). Again, with this comparison, no strong contrast is evident among the clades of these Ordovician crinoids. Only 10% of Middle Ordovician specimens and 7% of Late Ordovician specimens occur in state 2a, whereas 48% of Middle Ordovician specimens and 34% of the Late Ordovician specimens occur in state 3 (Tables 4–6). These data are consistent with the hypothesis that all of these Ordovician crinoids had only ligaments as connective tissue within the arms, as previously argued by Moore & Laudon (1943), Van Sant (1964), Ubaghs (1978), and Ausich & Baumiller (1993).

Table 7. Contingency table comparisons (Statview, Abacus Concepts, Inc.) between taphonomic patterns for Ordovician crinoids. Values correspond to the probability that the two taphonomic patterns being compared came from the same population. Note the null hypothesis, that the taphonomic patterns are indistinguishable, cannot be rejected for any of the comparisons (no values approach 0.05 or even 0.01). For comparisons in Middle Ordovician crinoids, see Table 4; for comparisons in Late Ordovician crinoids, see Table 5.

	Diplobathrids	Monobathrids	Disparids	Cladids	Rhombiferans
Middle Ordovician					
Diplobathrids	–	–	–	–	–
Monobathrids	0.78	–	–	–	–
Disparids	0.47	?	–	–	–
Cladids	0.92	?	0.38	–	–
Rhombiferans	0.41	?	?	0.61	–
Rhombiferans	0.41	?	?	0.61	–
Upper Ordovician					
Monobathrids	–	–	–	–	–
Disparids	–	0.68	–	–	–
Cladids	–	0.63	0.99	–	–

Discussion and conclusions

The two-ligament organization of intercolumnar and through-going ligaments present in living isocrinids was inferred in fossil isocrinids (Baumiller *et al.* 1995), and an analogous pattern was inferred for Lower Mississippian crinoids (Baumiller & Ausich 1992). This study, which extends the taphonomic approach to Middle and Late Ordovician crinoids and to one rhombiferan, suggests that the soft tissues in the stalks of those taxa may have been analogously distributed. The pattern of segments, although not as regular as in isocrinids, is significantly different from the random pattern expected from the broken-stick model; at present, this nonrandomness is best explained by differential tissue distribution. Therefore, the two-ligament organization is inferred to be a primitive feature of the Crinoidea. Because it is present in the one rhombiferan considered and because rhombiferans may be ancestral to crinoids (Ausich 1998), this organization may be a more primitive pelmatozoan characteristic. We suggest that this tissue organization may result from the heteromorphic growth style characterizing most Paleozoic crinoid stalks. If this tissue organization is primitive for crinoids, the very regular stalk segments and the specialized synostosial stalk articulations of isocrinid nodals (Breimer 1978; Baumiller & Ausich 1992) represent an additional evolutionary step superimposed on a preexisting pattern of soft-tissue organization; in this sense synostoses may be thought of as an exaptation of this preexisting column tissue organization.

The absence of muscles as an interplate connective tissue in the arms of Ordovician crinoids is consistent with studies of facet morphologies (Moore & Laudon 1943; Van Sant 1964; Ubaghs 1978) and taphonomic data

(Ausich & Baumiller 1993). Muscles between brachials apparently evolved as a derived adaptation in Devonian advanced cladids. This proved very successful for these crinoids, as advanced cladids dominated the Late Paleozoic (Baumiller 1994; Ausich *et al.* 1994) and gave rise to all post-Paleozoic crinoids (Simms & Sevastopulo 1993). Ordovician and most other Paleozoic crinoids apparently relied on factors other than muscles to move the arms (see discussion in Ausich & Baumiller 1993), so movement was passive or at best directed but very slow.

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