

A revised macroevolutionary history for Ordovician–Early Silurian crinoids

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Abstract.—Much of what is known about the long-term history of biodiversity and rates of taxonomic evolution in the fossil record derives from literature-based compilations of fossil stratigraphic ranges. It has been suggested that taxonomic and stratigraphic errors in these compilations are randomly distributed and, therefore, introduce no significant bias to macroevolutionary patterns. Here we compare a new, comprehensive global database of Ordovician and Early Silurian crinoids to Sepkoski's global genus compendium.

Approximately 44% of the crinoid genera resolved to substage in Sepkoski's compendium are taxonomically inaccurate (i.e., invalid, *nomina dubia*, or column genera) or have incorrect first and/or last occurrences. Errors in Sepkoski's compendium result from incomplete coverage of existing taxonomic work and incorrect stratigraphic correlations that, in some cases, are propagated throughout the taxonomic literature. Stratigraphic range errors are nonrandomly distributed among substages in Sepkoski's compendium. The result is underestimated richness in the Early Silurian and significantly overestimated rates of extinction in the Late Ordovician. There is no similar bias in Sepkoski's substage origination rates for crinoids.

At the stage-level of temporal resolution, Sepkoski's crinoid data are more accurate. In this case, only 32% of the compendium's crinoid genera contain some stratigraphic or taxonomic inaccuracy. However, errors still result in incorrect macroevolutionary patterns, particularly with respect to rate of origination in the Ashgill, which is significantly underestimated in Sepkoski's compendium. Genera described since the completion of Sepkoski's compendium have had relatively little effect on estimated rates of evolution at both stage and substage resolution.

These results suggest that macroevolutionary patterns among some taxa in Sepkoski's compilation may be significantly influenced by nonrandomly distributed taxonomic inaccuracies and stratigraphic range errors. In the case of the apparent end-Ordovician mass extinction among crinoids, the revised history reveals a dramatically reduced role for extinction at the substage-level of temporal resolution. At the stage level, Sepkoski's original compilation strongly exaggerates the excess of extinction over origination in the Ashgill. Although biases inherent in the stratigraphic record remain unaccounted for, removing taxonomic and stratigraphic errors in Sepkoski's compendium substantially changes our understanding of the nature of large-scale biotic change for an important Paleozoic taxon during the end-Ordovician.

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Introduction

Understanding the long-term history of biodiversity and rates of taxonomic evolution in the fossil record requires documenting the first and last appearances of fossil taxa. Gathering these data is a monumental task because of the sheer number of described fossil forms, uneven systematic treatment of organisms, and ongoing revision of the chronostratigraphic framework that enables the correlation and calibration of the geological record. Nevertheless, J. John Sepkoski Jr. completed such a compilation, first for marine families (Sepkoski 1981, 1982, 1992) and subsequently for all marine animal genera (Sepkoski 2002).

Although it is often assumed that such large-scale compilations of fossil data reflect relatively undistorted records of biological phenomena (e.g., Sepkoski 1981; Sepkoski et al. 1981; Raup and Sepkoski 1982; Wang 2003), there are many sources of error and bias that can alter biological signals in global taxonomic compilations. For example, errors intrinsic to compilations include taxonomic inaccuracies (Culver et al. 1987; Adrain and Westrop 2000; Smith and Jeffery 2000; Alroy 2002), incorrectly identified first and/or last occurrences (Adrain and Westrop 2000; Smith and Jeffery 2000; Jeffery 2001), and uneven sampling of the fossil record (e.g., Miller and

Foote 1996; Alroy et al. 2001). Biases extrinsic to compilations include variability in the total amount of preserved sedimentary rock (e.g., Raup 1976; Peters and Foote 2001, 2002; Smith 2001), geographic and environmental variation in the rock record (e.g., Ronov 1978; Ronov et al. 1980; Allison and Briggs 1993; Smith et al. 2001), and changes in the quality of preservation owing to taphonomic and diagenetic effects, such as aragonite dissolution (Cherns and Wright 2000; Wright et al. 2003) and degree of lithification (e.g., Donovan 2001). The forward and backward smearing of true variations in rates of origination and extinction due to incomplete preservation also contributes to the distortion of biological signals in face-value stratigraphic range data (Signor and Lipps 1982; Foote 2000). To test for, and possibly overcome, some of the biases inherent in the fossil record (Foote 2001, 2003), it is necessary to assume that stratigraphic and taxonomic errors in global compilations are randomly distributed and, therefore, introduce no systematic bias to macroevolutionary patterns. Unfortunately, very few studies have tested this assumption (Adrain and Westrop 2000; Jeffery 2001).

Here we examine genus richness and rates of origination and extinction among crinoids (Echinodermata) in Sepkoski's (2002) global compendium and compare these with a new, taxonomically and stratigraphically revised database for the Ordovician and Early Silurian. Crinoids were an important component of many post-Cambrian Paleozoic marine animal communities and the class constitutes one of the defining clades in Sepkoski's (1981) Paleozoic evolutionary fauna. This study focuses on the Ordovician and Early Silurian because this interval includes the second most severe mass extinction in the face-value fossil record of marine animals (Sepkoski 1981; Raup and Sepkoski 1982; Foote 2000) and because it has long been cited as pivotal in the evolution of many marine organisms, including crinoids (e.g., Baumiller 1993; Ausich et al. 1994; Eckert and Brett 2001).

Data and Methods

Sepkoski's (2002) global genus compendium includes 196 crinoid genera assigned to

the Ordovician and Early Silurian (Llandovery); 152 of these are fully resolved to substage within this interval. The new compilation, which was used to evaluate the accuracy of Sepkoski's taxonomic and stratigraphic data, has 264 genera from the same interval, including 63 genera described after the completion of Sepkoski's compendium (see supplemental data online). These new data were gathered by organizing all Ordovician through Llandovery crinoids into faunas (e.g., crinoids from the Pooleville Member of the Bromide Formation, the Brassfield Formation). We then used Webster's (2002) compilation to evaluate all species for validity and correct genus assignment. Similarly, we assessed the validity of all genera. In some instances, we made additional systematic changes and included unpublished data for faunal studies we knew to be near completion, such as the new Anticosti Island crinoid faunas (Ausich and Copper 2002, 2003). With faunal lists complete and taxonomically correct according to our present understanding, we determined the most up-to-date chronostratigraphic correlation of each stratigraphic unit. First and last occurrences were initially resolved to current Ordovician and Llandovery substages (Leslie and Bergström 1997; Fortey et al. 2000; S. M. Bergström personal communication 2003). However, in order to have clear comparisons to Sepkoski (2002), a common chronostratigraphic framework was needed. Because it is relatively straightforward to convert the substage scheme we followed to that used by Sepkoski (2002), this paper utilizes the Ordovician and Llandovery chronostratigraphic framework of Sepkoski (2002) (see Appendix 1 for additional information).

Macroevolutionary patterns derived from the new crinoid compilation were compared directly to those in Sepkoski's (2002) global genus compendium. This was done at both the stage and substage levels of temporal resolution in several ways. First, Sepkoski's crinoid data were taken at face value and the resultant time series of richness and rates of origination and extinction were calculated and compared with those derived from the new compilation. The types and magnitudes of Sepkoski's stratigraphic and taxonomic errors were then

quantified. After this initial comparison, Sepkoski's data were corrected by eliminating taxonomically invalid genera, *nomina dubia*, and column genera and by correcting any stratigraphic errors in the first and/or last occurrences of valid genera. Macroevolutionary patterns in the corrected Sepkoski compendium were also compared with those in the new compilation. Differences between Sepkoski's corrected compendium and the new compilation reflect the influence of genera that were either erroneously omitted from the compendium or, more commonly, described after its completion. Thus, this study shows what Sepkoski's original genus compendium reveals about the macroevolutionary history of crinoids, what would have been revealed if Sepkoski had not included any taxonomic or stratigraphic errors, as they are now understood, and how newly described genera have modified macroevolutionary patterns among crinoids.

To test whether the differences in macroevolutionary patterns between Sepkoski's compendium and the new crinoid database are greater than expected on the basis of randomly distributed stratigraphic range errors, the observed frequency and magnitudes of stratigraphic range errors were randomly distributed among genera in Sepkoski's corrected compendium. Time series of richness, origination, and extinction were then calculated for these simulated error-laden data. This process was repeated 1000 times to generate a distribution of richness, origination, and extinction values expected in each substage under a model of randomly distributed stratigraphic ranges errors.

Macroevolutionary Patterns: Substage Resolution

Eighty of Sepkoski's crinoid genera (39 percent of all genera; 50 percent of those that were resolved to substage by Sepkoski) are valid and have correct first and last occurrences at substage precision. By comparison, Adrain and Westrop (2000) found only approximately 30 percent of Sepkoski's Ordovician and Silurian trilobites to be accurate. Thus, crinoids appear to be more accurately resolved than trilobites in Sepkoski's compilation.

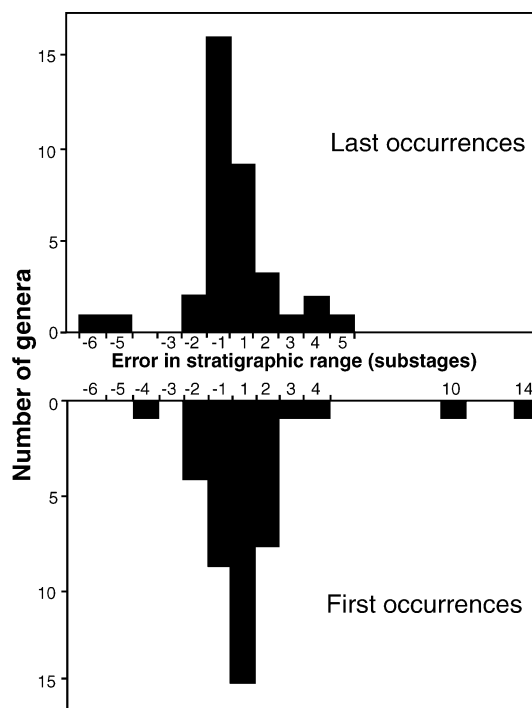


FIGURE 1. Frequency distributions of magnitude and direction of stratigraphic range error among valid genera resolved to substage in Sepkoski's genus compendium. Errors are calculated as the number of substages between Sepkoski's originally defined range endpoint and the revised range endpoint. Positive errors correspond to range endpoints that are too young in Sepkoski's original compendium; negative errors correspond to range endpoints that are too old.

Similar to Ordovician–Silurian trilobites (Adrain and Westrop 2000), crinoids with incorrect first and/or last occurrences in Sepkoski's compendium are generally incorrect by only one or two substages, but some genera have first or last occurrences that are more grievously inaccurate (Fig. 1). Substage errors in Sepkoski's compendium are summarized in Table 1.

Figure 2 shows the time series of total crinoid genus richness for substages in Sepkoski's compilation and for the newly compiled data. Also shown is the time series derived by simply correcting Sepkoski's data, which excludes all genera described after the completion of Sepkoski's compendium. All three time series show similar genus richness histories until approximately the Caradoc. After this time, there is a marked divergence between Sepkoski's compendium and the newly com-

TABLE 1. Summary of substage errors for crinoids in Sepkoski's global genus compendium. Abbreviations: FO, first occurrence; LO, last occurrence; JJS, Sepkoski compendium. "Resolved" indicates genera resolved to substage in Sepkoski's compendium. "Unresolved" indicates genera with at least one occurrence unresolved to substage in Sepkoski's compendium. Numbers in parentheses correspond to the number of genera with an unresolved first or last occurrence that is incorrect at the stage level of temporal resolution. All genera that were incorrectly located in or out of the interval have a first and/or last occurrence that is incorrect at the stage level of temporal resolution.

Type of error	No. of genera
Resolved, correct FO incorrect LO	20 (11)
Resolved, correct LO incorrect FO	9 (2)
Resolved, incorrect FO and incorrect LO	14 (8)
Resolved invalid, <i>nomen dubium</i> , and column genera	11
Unresolved LO, correct FO	13 (2)
Unresolved LO, incorrect FO	10 (1)
Unresolved FO, correct LO	6 (4)
Unresolved FO, incorrect LO	2 (1)
Unresolved FO and LO	25 (5)
Unresolved invalid and <i>nomen dubium</i> genera	10
Unresolved genera located out of interval in JJS	5
Unresolved genera incorrectly located in interval in JJS	2
Resolved genera located out of interval in JJS	8
Resolved genera incorrectly located in interval in JJS	1

piled data. This is especially true for the Early Silurian, where crinoid richness in the new compilation appears to be as much as eight times greater than suggested by Sepkoski's compendium. Revising the compendium data ameliorates this problem by extending the ranges of some genera into the Llandovery and by resolving genera to substage within

the Llandovery, but there is still a large discrepancy between Sepkoski's revised data and the new compilation in the Late Ordovician and Early Silurian. This reflects the fact that most of the 63 genera described since the completion of Sepkoski's compendium are Ashgill to Early Silurian in age.

The time series of genus richness shown in Figure 2 are broadly consistent with other work. After completion of the new genus compendium utilized here, Sprinkle and Guensburg (2004) published a new compilation of crinoid species richness through the Ordovician. These data yield a species richness pattern that is, overall, quite similar to the genus richness data presented in Figure 2. However, the species-level data lack some features of the genus-level data presented here, most notably, a mid-Ashgill peak in richness.

Figure 3 compares the time series of per-lineage-million-year (LMyr) extinction and origination rates (Foote 2000, 2001) for crinoids in Sepkoski's compendium, Sepkoski's corrected compendium, and the new compilation. In keeping with expectations based on the well-known end-Ordovician mass extinction (Donovan 1988, 1989; Eckert 1988), Sepkoski's original compendium shows a dramatic increase in extinction rate among crinoids during the middle Ashgill (Fig. 3A). Extinction rate declines into the late Ashgill in Sepkoski's orig-

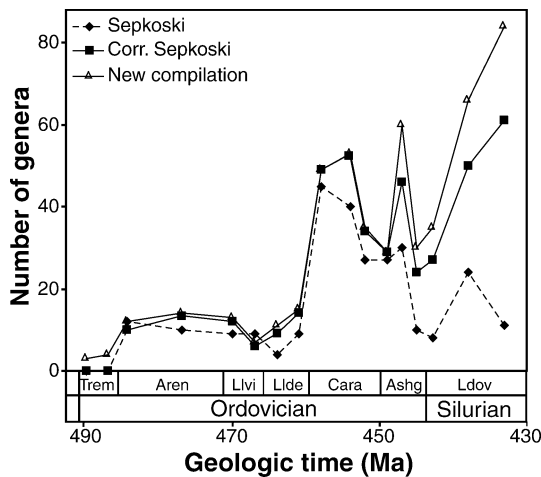


FIGURE 2. Time series of global crinoid genus richness for substages in the Ordovician and Early Silurian. Data are from Sepkoski's original compendium, Sepkoski's corrected compendium, and the new compilation, which includes genera described since the completion of Sepkoski's compendium. The difference between Sepkoski's corrected compendium and the new compilation reveals the effect that additional field collecting has had on the overall richness pattern.

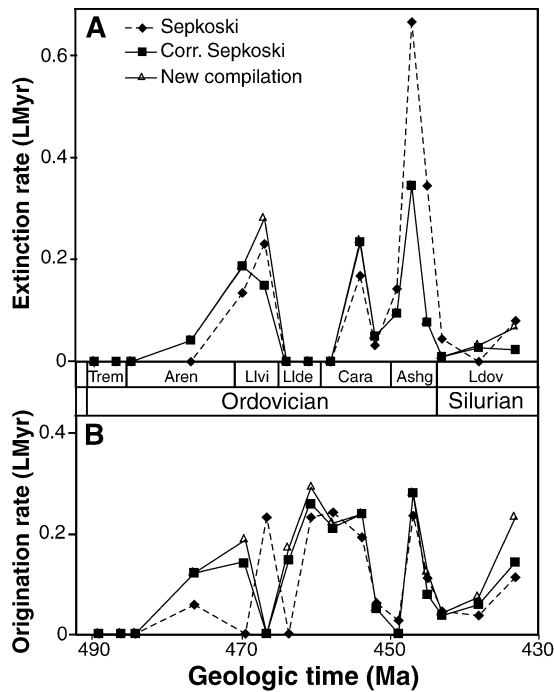


FIGURE 3. A, Time series of global per-lineage-million-year (LMyr) extinction rates among crinoids for substages in the Ordovician to Early Silurian. B, Time series of per-LMyr origination rates for same data. Time series as in Figure 2. There is a large excess of extinction during the late Ashgill in Sepkoski's original compendium. Note that there is little difference between the revised Sepkoski compendium and the new compilation in most substages, indicating that newly described genera have had relatively little impact on estimated rates of evolution. Discrepancies among the compilations in the Early and Middle Ordovician are due primarily to the relatively small number of genera in this interval (Fig. 2).

inal substage data, but the extinction rate for this substage is still very high in comparison to other intervals. Thus, the end-Ordovician mass extinction that appears in Sepkoski's global compendium for all marine animals is borne out very strongly among crinoids. However, errors and unresolved genera in Sepkoski's data result in severely overestimated rates of extinction in these two substages.

In Sepkoski's revised data and in the new compilation, extinction rate increases during the middle Ashgill, but the increase is approximately one-half of that observed in Sepkoski's original compendium. The extinction rate during the late Ashgill is actually quite low when the data are corrected. In all other substages, there is comparatively little difference in extinction rate among the three com-

pilations (Fig. 3A). Thus, Sepkoski's compendium exaggerates the magnitude of extinction only in the last two substages of the Ashgill. Notice that for most substages in Figure 3A there is virtually no difference between Sepkoski's corrected compendium and the new compilation. This reflects the fact that many of the genera that were not included in Sepkoski's compendium are restricted to single substages and are, therefore, not used in estimating rates of evolution (Foote 2000).

In contrast to the substage extinction results, there is no similarly dramatic inconsistency between Sepkoski's original substage rates of origination and the rates of origination estimated on the basis of the new compilation or Sepkoski's corrected compendium. Figure 3B shows the largely comparable time-series of origination for each of the three data sets. There is considerable discrepancy between Sepkoski's original compendium and the new compilation for some Early and Middle Ordovician substages, but this occurs primarily because the rather small number of genera in this interval (Fig. 2) exacerbates errors in Sepkoski's data. Origination rates in Sepkoski's corrected compendium and the new compilation are indistinguishable in most substages, indicating that, as with extinction, newly described genera have had relatively little impact on estimated rates of taxonomic origination during this interval. The exception to this is the late Llandovery (Telychian), where newly described species have extended the ranges of genera from the Wenlock into the late Llandovery, thereby increasing the estimated rate of origination for this interval.

It is possible to determine exactly why rates of extinction and origination were incorrectly or correctly estimated in Sepkoski's original compendium. Figure 4 shows the difference between Sepkoski's compendium and the corrected compendium for each of the four characteristic types of taxa (Foote 2000) in each substage. Bars below the zero-line correspond to underestimates in Sepkoski's compendium; bars above the line indicate groups of genera that Sepkoski overestimated. Foote's (2000) survivorship-based evolutionary rates depend on the ratio of taxa that range through an interval to those that cross the bottom interval

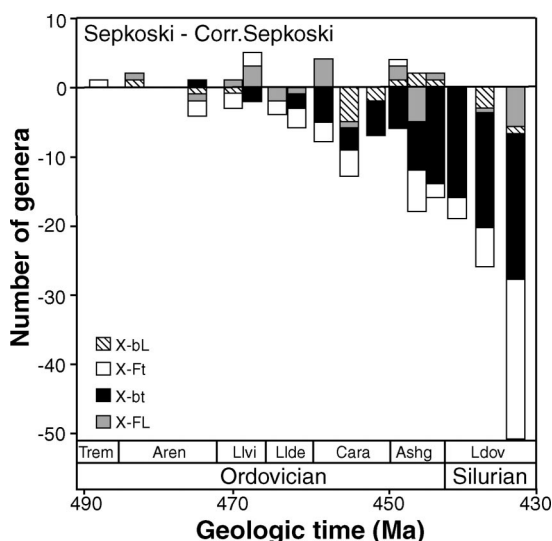


FIGURE 4. Difference between Sepkoski's original compendium and the corrected compendium for each of the four characteristic types of taxa (Foote 2000) in each substage. Bars below the zero-line indicate a deficit in the original compendium; bars above the line indicate a surplus. X-FL, genera with first and last occurrence in interval; X-Ft, genera with first occurrence in interval and last occurrence after interval; X-bL, genera with first occurrence before interval and last occurrence after interval; X-bt, genera with first occurrence before interval and last occurrence in interval. See text for discussion.

boundary (extinction) or top interval boundary (origination). Thus, it is possible, for example, to overestimate the number of taxa that go extinct in an interval and still obtain the correct extinction rate if the number of through-ranging taxa is also overestimated.

In the case of extinction rates, Sepkoski's original compilation overestimated the number of genera that crossed into the last two Ashgill substages and went extinct, as well as underestimated the number of through-ranging genera. Both of these errors serve to exaggerate extinction rate. In the case of origination rate in the last two Ashgill substages, Sepkoski underestimated the number of genera that first appeared in these substages, but he also underestimated the number of through-ranging genera. These errors, in effect, offset each other with respect to estimating rates of origination.

To test whether evolutionary rates in Sepkoski's original compendium are within the range expected in the case of randomly distributed stratigraphic range errors, a simula-

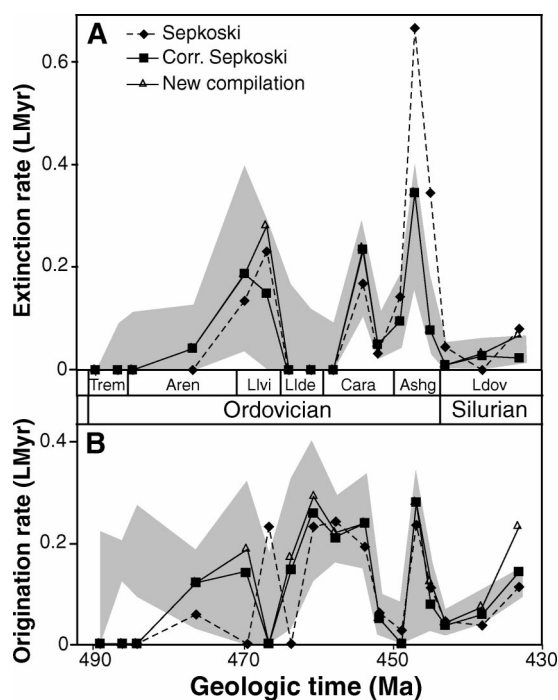


FIGURE 5. Results of randomly distributing the observed substage stratigraphic range errors among genera in Sepkoski's corrected compendium. Randomization was repeated 1000 times. Shaded regions demark two standard deviations about the mean rate expected in each substage. Distributions with mean rate greater than approximately 0.05 are approximately normally distributed. The shaded region should be compared with Sepkoski's original compendium (dotted line). Note that rates in Sepkoski's original compendium fall within the shaded region for most substages. However, Sepkoski's rates of extinction in the last two substages of the Ashgill fall far above the range of values expected on the basis of randomly distributed errors. Early and Middle Ordovician rates falling outside of the shaded interval are primarily due to the small numbers of genera in this interval (Fig. 2). See text for discussion.

tion analysis was performed (see "Data and Methods"). These results indicate that Sepkoski's estimated rates of evolution in most substages are within the range of values expected on the basis of randomly distributed stratigraphic range errors of the frequency and magnitude observed in Sepkoski's data (Fig. 5). However, middle and late Ashgill extinction rates in Sepkoski's original compendium are far outside the range of the expected distributions, indicating that random range errors are very unlikely ($p < 0.001$) to yield such aberrant estimated extinction rates in these two substages. Thus, Sepkoski's data appear to exhibit a nonrandom concentration of un-

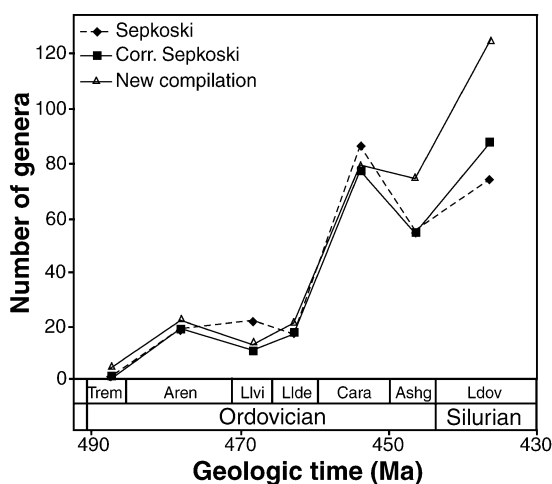


FIGURE 6. Time series of global crinoid genus richness for stages in the Ordovician and Early Silurian, as in Figure 2.

resolved taxa and stratigraphic range errors that artificially exaggerate apparent extinction rates in the late Ashgill. In the Early Ordovician, some of Sepkoski's origination rates fall outside of the expected distributions primarily because of the rather small number of genera that are known from the clade's early history (Fig. 2).

Macroevolutionary Patterns: Stage Resolution

At the coarser temporal resolution of stratigraphic stages, Sepkoski's data are, not surprisingly, more accurate; 140 crinoid genera (68 percent) are valid and have ranges correctly resolved to stratigraphic stage in Sepkoski's compendium. Figure 6 shows the time series of genus richness for Ordovician and Early Silurian stages. Like the substage analyses presented in Figure 2, the three compilations yield similar richness histories up to the Caradoc. After this stage, richness is higher in the new compilation because of the preferential concentration of newly described genera in the Ashgill and Early Silurian.

Figure 7A shows the time series of per-lineage-million-year rates of extinction among crinoids for stratigraphic stages in the Ordovician and Early Silurian. In contrast to the substage-level analyses (Fig. 3A), crinoid extinction rate at the end-Ordovician is not exaggerated in Sepkoski's original stage-level

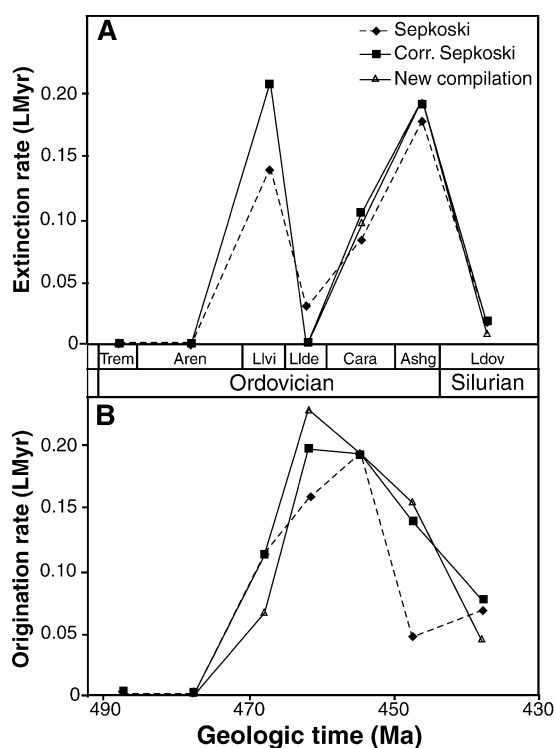


FIGURE 7. A, Time series of global per-lineage-million-year (LMyr) extinction rates among crinoids for stages in the Ordovician to Early Silurian. B, Time series of per-LMyr origination rates for same data. Time series as in Figure 3. Note that Sepkoski's original compendium severely underestimates origination rate in the Ashgill, leading to a large and incorrect excess of extinction over origination in this stage. See text for discussion.

compendium. In fact, all three data sets yield similar extinction histories. The new compilation and Sepkoski's corrected compendium, in particular, yield virtually identical extinction time series, indicating that additional taxonomic work and field collection has had little influence on the stage-level extinction pattern.

Although the overall extinction history appears to be rather accurately captured in Sepkoski's original stage-level crinoid data, origination is not so faithfully recorded. Figure 7B shows the time series of rates of genus origination for each of the three compilations. Sepkoski's original genus compendium yields a stage-level origination history that differs substantially from the corrected compendium and the new compilation. In particular, Sepkoski's original compendium underestimates origination rate by approximately a factor of three in the Ashgill, which results in an erro-

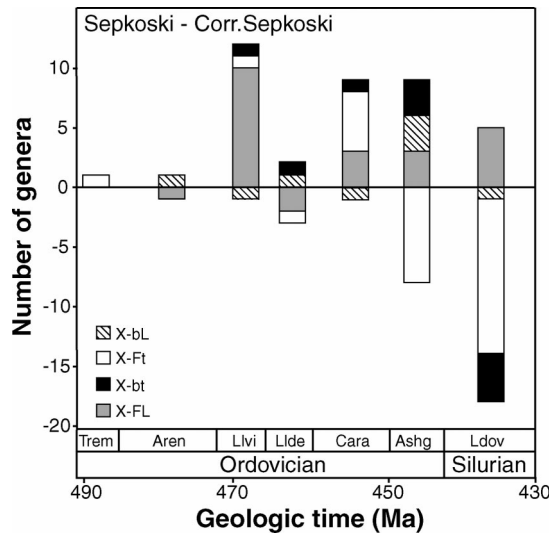


FIGURE 8. Difference between Sepkoski's original compendium and the corrected compendium for each of the four characteristic types of taxa (Foote 2000) in each stage, as in Figure 5.

neous excess of extinction over origination in this stage. In the Ashgill of the corrected Sepkoski compendium and the new compilation, extinction rate is only slightly greater than origination rate.

As in Sepkoski's substage data, it is possible to determine exactly how rates of evolution were either correctly or incorrectly estimated in Sepkoski's data. Figure 8 shows the difference between Sepkoski's compendium and the corrected compendium for each of the four characteristic types of taxa (Foote 2000) in each stage, as in Figure 4. Sepkoski did, in fact, overestimate the number of extinctions in the Ashgill, which is consistent with the substage results presented above, but the Sepkoski compendium also overestimated the number of taxa that range through the Ashgill. Because these errors work in opposing directions in the calculation of extinction rates, Sepkoski's original compendium provides a rather accurate extinction rate estimate despite the fact that the actual number of extinctions in the Ashgill was exaggerated. Origination rate, on the other hand, is severely underestimated in Sepkoski's data because the number of taxa that first occur in the Ashgill and then pass into the Early Silurian was underestimated and because the number of through-ranging

genera was overestimated. These two errors both contribute to underestimated rates of origination during the Ashgill and lead to the discrepancy illustrated in Figure 7B.

Discussion

Sources of Error.—Crinoids from the Ordovician and Early Silurian have received considerable systematic treatment since Sepkoski stopped working on the compendium, and the revised data presented here are improved (1) by correcting taxonomic and stratigraphic errors, and (2) by the addition of newly discovered genera. One might be tempted to assume that any discrepancy between Sepkoski's compendium and the new compilation is due to the addition of newly described crinoid genera. However, we have shown that the corrected Sepkoski compendium, which excludes all genera that were not originally included in the compendium, yields macroevolutionary patterns that are more similar to those in the new compilation than they are to patterns in Sepkoski's original data. Thus, newly described crinoid faunas have had relatively little impact on many macroevolutionary patterns among Ordovician and Early Silurian crinoids.

Discrepancies between Sepkoski's original compendium and the corrected compendium are due primarily to stratigraphic range inaccuracies and taxonomic errors, which are inevitable in literature-based compilations. The most common errors were incorrect first and last occurrences within the Ordovician to Llandovery (Table 1) and, as discussed above, deviations by one substage were most common (Fig. 1). To illustrate the contrast between the Sepkoski compendium and the new compendium and to reveal the sources of taxonomic and stratigraphic errors, we analyzed the 52 crinoid genera beginning with the letter *A*, *B*, or *C* in Sepkoski's (2002) compendium (genera starting with *A*, *B*, or *C* were chosen as a workable arbitrary sample). The results of this analysis are presented in Table 2 and Appendix 2.

Twenty-nine (56%) of the 52 "*A*, *B*, and *C*" crinoid genera in Sepkoski's compendium were correct, although not all of the genera were resolved to the substage level. Nine dis-

TABLE 2. Analysis of the generic status and stratigraphic ranges for the 52 crinoids in Sepkoski's (2002) compendium that begin with the letter *A*, *B*, or *C*. 1998 is taken as the date for Sepkoski's completion of the compendium; and at this time, 73% of the Ordovician–Llandovery crinoid genera beginning with *A*, *B*, or *C* were correct (either resolved or unresolved to substage level). Work since 1998 has reduced the accuracy to 56%. A detailed discussion of each genus is presented in the Appendix. See text for discussion.

Correct genera	
1. Resolved to substage	23
2. Resolved to stage	6
Genera with stratigraphic range errors	
1. Taxonomic revisions known prior to 1998	6
2. Taxonomic revisions after 1998	4
3. Stratigraphic correlation changes prior to 1998	3
4. Stratigraphic correlation changes after 1998	2
5. Unable to isolate cause of error	3
Invalid genera	
1. Taxonomic revisions prior to 1998	
a. Genus designated as a junior synonym	2
2. Taxonomic revisions during or after 1998	
a. Genus designated a <i>nomen dubium</i>	2
b. Genus occurrence eliminated owing to questionable assignment	1

crepancies (17%) arose from taxonomic or stratigraphic changes made after the Sepkoski (2002) compendium was completed and were, therefore, unavoidable in 1998. However, 11 genera (21%) had taxonomic or stratigraphic range errors that Sepkoski could have incorporated into the compendium (Table 2, Appendix 2). In the “*A*, *B*, and *C*” sample, and throughout Sepkoski's crinoid Ordovician–Early Silurian data, avoidable error occurred because old entries were not updated as ongoing systematic changes and stratigraphic revisions were published.

There are many other reasons for incorrect first and last occurrences in Sepkoski's compendium, and stratigraphic errors could have found their way into Sepkoski's compendium in several ways. Simple bookkeeping mistakes are probably the least common error type, although three genera in the “*A*, *B*, and *C*” sample may be examples. In the case of Ordovician to Llandovery crinoids, another very important source of error is the history of the development of the chronostratigraphic framework used to establish genus range endpoints.

Chronostratigraphic subdivisions and correlations to specific stratigraphic units have undergone numerous revisions that continue today. A “correct” correlation of a crinoid-bearing rock unit in 1950 may have changed one to several times through the latter half of the twentieth century. Which age determina-

tion would have been entered into the final version of the Sepkoski compendium? Unfortunately, summary literature inconsistently incorporates these needed revisions, so that outdated age correlations may be perpetuated in the literature, or worse, errors may become additive.

Crinoids from the Cincinnatian of the Cincinnati Arch region clearly illustrate this problem. Generations of geologists have been raised with the notion that Ordovician rocks from the world-renowned Cincinnatian Arch region are equivalent to the Late Ordovician. However, we now know this to be incorrect. The Cincinnatian is now best correlated only to the upper part of the global Late Ordovician. Specifically, the Kope Formation is Marshbrookian to Onnian (Caradoc), the Maysvillian is Onnian to Pugsillian (Caradoc and Ashgill), and the Richmondian is Rawtheyan (Ashgill). In much of the literature and on many museum labels, however, all Cincinnatian crinoids are designated as only “Upper Ordovician.” In the literature, confusion also exists with placement of the Richmondian (upper part of the Cincinnatian). For example, in 1943, Bassler and Moodey compiled the first, modern bibliographic index of Paleozoic crinoids. At this time, these authors considered the Richmondian to be either Ordovician or Early Silurian (Bassler and Moodey 1943: pp. 40–42). Entries in the index reflect this age

assignment, with, for example, *Canistrocrinus richardsoni* (Wetherby) (p. 355) and *Gaurocrinus nealli* (Hall) (p. 483) being assigned to the Early Silurian. This is the case for Richmondian crinoids (and presumably many other taxa) throughout North America. Unfortunately, some of these same errors have been carried forward into the most recent bibliographic index (Webster 2002). Examples in Webster (2002) include *Canistrocrinus typus* (Wachsmuth and Springer), *Cupulocrinus minimus* Springer, *Cupulocrinus polydactylus* (Shumard), and *Plicodendrocrinus casei* (Meek).

Systematic errors in Sepkoski's (2002) compendium include genera that we now consider to be *nomina dubia* or junior synonyms. All five *nomina dubia* were so designated after the completion of Sepkoski's compendium and were therefore unavoidable in 1998. Six of the nine junior synonyms, on the other hand, were established prior to completion of the compendium and should have been accurately reflected by Sepkoski (2002).

These results demonstrate that several kinds of errors occur in taxonomic compendia. Many of these errors are inevitable without periodic confirmation of the accuracy of both stratigraphic and taxonomic data using sources that are independent of the original taxonomic literature and summary work. We attempted to minimize errors in the assembly of the new Ordovician–Llandovery crinoid compilation by tying individual species occurrences to specific stratigraphic units. Once currently valid taxa were assigned to stratigraphic units, modern chronostratigraphic correlation of these units determined genus ranges. Because both taxonomy and stratigraphic correlations are being continually refined, we believe that this approach is essential when trying to accurately measure large-scale patterns of biodiversity and rates of evolution in the fossil record.

Macroevolutionary Patterns.—At both the stage and substage levels of temporal resolution, Sepkoski's compilation erroneously yielded a large excess of extinction over origination at the end-Ordovician. However, it is interesting that the reason for the excess differs depending on the temporal resolution of analysis. For substages, extinction rates are

strongly exaggerated in the late Ashgill, but rates of origination are generally correct (exceptions occur in the Early and Middle Ordovician, where origination rates often deviate because the total number of genera is rather small). The opposite is true at the stage level of temporal resolution; extinction rates are estimated rather accurately in Sepkoski's original stage-level data, but rates of origination in the Ashgill are substantially underestimated. In both cases, the number of taxa going extinct in the Ashgill was exaggerated, but in the stage-level data, this error was offset by a similar overestimate of the number of through-ranging genera.

After Sepkoski's crinoid genera are revised and incorporated back into the complete compilation for all marine animal genera, the estimated global rates of extinction for all animals during the last two substages of the Ashgill drops by approximately 5%. Crinoids constitute about 5% of the total number of animal genera in Sepkoski's Late Ordovician data. Thus, if the errors in Sepkoski's crinoid data are symptomatic of those that are present in other taxa, it is possible that the magnitude of the end-Ordovician global extinction is exaggerated in Sepkoski's substage data. Similarly, Jeffery (2001) found that extinction rate among echinoids at the end-Cretaceous was 50% greater in Sepkoski's data than it was in a taxonomically and stratigraphically revised compilation. Unfortunately, it was not clear whether all stratigraphic intervals had erroneously high rates, which would not affect the relative severity of the extinction, but Jeffery's (2001) results suggest the possibility that taxonomic and stratigraphic errors in other taxa may be nonrandomly concentrated around apparent mass extinction intervals. This is perhaps not surprising given the difficulties of global correlation that often accompany mass extinction intervals.

The extent to which these results can be extrapolated to other taxa is, however, uncertain. Adrain and Westrop (2000) found that Sepkoski's compilation had a very large number of errors among trilobite genera (approximately 70%). It is possible that errors are less common among crinoids because the number of taxonomically useful crinoid assemblages is

more strongly limited by taphonomic factors and because comparatively few workers have contributed to crinoid taxonomy. Regardless of the reason for the higher error rate among trilobites, Adrain and Westrop (2000) found that Sepkoski's error-laden data and their independently compiled trilobite data yielded similar macroevolutionary patterns (Adrain and Westrop 2002: Fig. 3). The authors therefore concluded that the taxonomic and stratigraphic errors in Sepkoski's compendium are of little consequence to several large-scale macroevolutionary patterns. This is at odds with our results for Ordovician and Early Silurian crinoids, where we find relatively few errors with substantial macroevolutionary significance. The reasons for the discrepancy between trilobites and crinoids remain unclear, but it suggests that the reliability of Sepkoski's data for one taxon cannot easily be generalized to others. More studies like that of Adrain and Westrop (2000) and this one are needed for other taxa during the end-Ordovician, as well as other putative mass extinction intervals.

Although the biological significance of the crinoid richness, extinction, and origination patterns documented here remains unclear because underlying temporal and spatial variation in the stratigraphic record (e.g., Raup 1976; Peters and Foote 2001, 2002; Smith 2001) remains unaccounted for, these results substantially revise the macroevolutionary history of an important constituent of Paleozoic marine animal communities. Most studies of the end-Ordovician extinction have suggested that a two-step biotic crisis (end-Rawtheyan and end-Hirnantian) is preserved in the face-value fossil record (for crinoids: Eckert 1988; Donovan 1988, 1989; general summary: Sheehan 2001). A two-phased extinction pattern is also recorded in Sepkoski's original substage data for crinoids (Fig. 3). The end-Ordovician has also been identified as a significant interval for crinoids because it marks the transition from the Early to Middle Crinoid Macroevolutionary Fauna (Ausich et al. 1994). A revised interpretation of this faunal change will be discussed in a subsequent study. However, the present study demonstrates that both the corrected Sepkoski compendium and the new

compilation reveal a single, substantially smaller peak in crinoid extinction during the middle Ashgill (Rawtheyan). Crinoids are not alone in showing this face-value pattern, as graptolites also exhibit one apparent extinction episode prior to the end-Hirnantian (Mitchell et al. 2002). Are crinoids and graptolites unusual in showing a single apparent pulse of extinction that precedes the Late Ashgill? We do not yet know, but this study is an essential first step toward a more refined understanding of the history of biodiversity and rates of evolution during a critical period in the evolution of marine animals.

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Appendix 1

Chronostratigraphic Subdivisions

Ordovician substages are adopted from Fortey et al. (2000) with additional modifications from Ross et al. (1982) and Leslie and Bergström (1997). The Ordovician is currently divided into the following (Sepkoski substages in parentheses): Tremadoc, *flabelliforme-incipiens* zone (Trem-l), and *here-serratus* zone (Trem-u); Arenig, *extensus* zone (Aren-l) and *hirundo* zone (Aren-u); Llanvirn, *bifidus* zone Llvi-l, *murchisoni* zone (Llvi-u), and *teretiusculus* zone (Llde-l); Caradoc, *gracilis* zone (Llde-u), Costian (lower part of Cara-l), Harnagian (upper part of Cara-l), Soudleyan (lower part of Cara-m), Marshbrookian (upper part of Cara-m), Actonian (lower part of Cara-u), Onnian (upper part of Cara-u); Ashgill, Pusgillian (Ashg-l), Cautleyan (lower part of Ashg-m), Rawtheyan (upper part of Ash-m), Hirnantian (Ashg-u). Silurian substages are the same as those used by Sepkoski, from oldest, Rhuddanian, Aeronian, and Telychian.

Appendix 2

Analysis of Genera Beginning with the Letter A, B, or C (A Workable Arbitrary Sample) from the Sepkoski (2002) Compendium

“Up” and “down” refer to movement of first occurrence (FO) or last occurrence (LO) to either younger (up) or older (down) substages. If FO or LO is not explicitly mentioned, then it is correct in Sepkoski 2002.

- Abacocrinus* Angelin—FO moved down at least one substage; LO unresolved but correct to stage. This genus is currently recognized from the upper Llandovery on the basis of an unpublished monograph on Anticosti Island crinoids by W.I.A.
- Abludoglyptocrinus* Kolata—LO moved down five substages in the new compilation. Kolata (1982) defined this genus, which includes five species, and reported a range from the Middle Ordovician (Champlainian) to Early Silurian (Alexandrian). This is the range cited by Sepkoski (2002). Four of the included species are Middle Ordovician and one, *A. insperatus* (Rowley), is Early Silurian. In 1987, Ausich re-evaluated Late Ordovician to Early Silurian crinoids from Missouri and, among other things, reassigned *A. insperatus*

to *Ptychocrinus insperatus* (Rowley). This crinoid is also now considered to be of Hirnantian age, which restricts the occurrence of this genus to the Harnagian to Marshbrookian. This revision is not included in Sepkoski 2002.

- Acacocrinus* Wachsmuth and Springer—This citation is correct in Sepkoski 2002.
- Acolocrinus* Kesling and Paul—This citation is correct in Sepkoski 2002.
- Aethocrinus* Ubahgs—FO moved up by one substage and LO moved up by one substage in the new compilation. These stratigraphic revisions occurred after 1998, and further revisions are anticipated.
- Agostocrinus* Kesling and Paul—This citation is correct in Sepkoski 2002.
- Aithriocrinus* Donovan and Veltkamp—This citation is correct in Sepkoski 2002.
- Alisocrinus* Kirk—This citation is correct in Sepkoski 2002.
- Allocrinus* Wachsmuth and Springer—FO moved down by one substage, LO unresolved but correct to stage. Prior to 1981 *Allocrinus* was confined to rocks younger than the Llandovery, but Witzke and Strimple (1981) described two species in this genus (one new and one left in open nomenclature allied to an existing species) from the upper Llandovery. This range extension is not included in Sepkoski 2002.
- Allozygocrinus* Witzke and Strimple—This genus is correctly placed in the Llandovery in Sepkoski 2002, but it is not resolved to substage.
- Amarsupiocrinus* Frest—This genus is correctly placed in the Llandovery in Sepkoski 2002, but it is not resolved to substage.
- Anarchocrinus* Jaekel—This genus is herein treated as a *nomen dubium*.
- Anomalocrinus* Meek and Worthen—FO moved up two substages in the new compilation. Webster (2002) listed three species in *Anomalocrinus*, the oldest being? *A. antiquus* Guensburg from the lower Caradoc. For the present analysis, we eliminated? *A. antiquus* because of the uncertainty of its generic assignment. The other two species are from the Maysvillian of the greater Cincinnati area, and their age assignment is correct.
- Anthracoocrinus* Strimple and Watkins—This citation is correct in Sepkoski 2002.
- Anulocrinus* Ramsbottom—FO moved up four substages, and LO moved up more than four substages in the new compilation. Today only two species of *Anulocrinus* are considered valid, *A. thraivensis* Ramsbottom (middle Ashgill) and *A. simplex* Springer (Ludlow). Brower (1982) reassigned four Middle Ordovician species of *Anulocrinus* to *Cremacrinus*, and one of these ranged down into the Caradoc. So, Sepkoski (2002) did not incorporate the revisions of Brower (1982) and failed to account for *A. simplex*, which was assigned to *Anulocrinus* in 1962.
- Apodasmocrinus* Warn and Strimple—This citation is correct in Sepkoski 2002.
- Archaeocalyptocrinus* Witzke and Strimple—This genus is correctly placed in the Llandovery in Sepkoski 2002, but it is not resolved to substage.
- Archaeocrinus* Wachsmuth and Springer—FO unresolved but correct to stage; LO moved down one substage in the new compilation. *Archaeocrinus* is a general genus name used during the early study of crinoids. Through the years, 23 species have been named, but 12 of these have been subsequently reassigned. We have been unable to isolate the reason why Sepkoski (2002) had this genus in the lower Ashgill.
- Archaeotaxocrinus* Lewis—LO moved up by two substages. This change is from stratigraphic correlation changes since the Sepkoski (2002) compendium was completed.
- Atactocrinus* Weller—This citation is correct in Sepkoski 2002.

- Atopocrinus* Lane—This genus was designated a junior synonym of *Othneiocrinus* Lane by Lane and Moore (1978).
- Atyphocrinus* Ulrich—This genus was designated a junior synonym of *Dystactocrinus* Ulrich by Warn and Strimple (1977).
- Baerocrinus* Volborth—Considered a *nomen dubium* by Ausich (1998).
- Balacrinus* Ramsbottom—This citation is correct in Sepkoski 2002.
- Bikocrinus* Ausich—This citation is correct in Sepkoski 2002.
- Bolicrinus* Witzke and Strimple—This genus is correctly placed in the Llandovery in Sepkoski 2002, but it is not resolved to substage.
- Bromidocrinus* Kolata—This citation is correct in Sepkoski 2002.
- Caelocrinus* Xu—This genus was moved into the Middle Silurian by Webster (2002).
- Calceocrinus* Hall—FO is correct in Sepkoski 2002, but the LO is unresolved.
- Caleidocrinus* Waagen and Jahn—FO moved down one substage. Botting (2003) described this taxon from older strata. In addition to this change, Donovan (1985) divided *Caleidocrinus* into two subgenera, *Caleidocrinus* (*Caleidocrinus*) and *Caleidocrinus* (*Huxleycrinus*). These have distinct stratigraphic ranges, Cara-l to Cara-m and Llvi-l to Llvi-u, respectively, and should be treated as separate generic-level taxa even if kept at subgeneric rank.
- Canistrocrinus* Wachsmuth and Springer—This citation is correct in Sepkoski 2002.
- Carabocrinus* Billings—This citation is correct in Sepkoski 2002.
- Carpocrinus* Müller—FO moved up one substage, and LO, which is outside of the interval of interest in this study, is unresolved. Apparently, this was a clerical error, as Witzke and Strimple (1981) described the only Llandovery occurrence of *Carpocrinus* as from the “mid Late Llandovery.”
- Cataraquicrinus* Kolata—FO and LO moved up one substage in the new compilation. The stratigraphic position of the Gull River Formation was revised by Leslie and Bergström (1997).
- Catatonocrinus* Brett—FO and LO moved up by three substages. This genus is erroneously placed in the lower Llandovery, presumably as a clerical error, because the only species assigned to this genus is known only from the Wenlock.
- Celtocrinus* Donovan and Cope—This citation is correct in Sepkoski 2002.
- Chirocrinus* Angelin—FO moved to the Wenlock. This genus is erroneously placed in the Llandovery because Ausich (1984) removed *Calceocrinus insertus* from *Chirocrinus*, thus restricting the occurrence of this genus to the Wenlock. Furthermore, both the FO and LO were unresolved to substage in Sepkoski 2002.
- Cincinnatiocrinus* Warn and Strimple—This citation is correct in Sepkoski 2002.
- Claviculacrinus* Donovan—This citation is correct in Sepkoski 2002.
- Cleiocrinus* Billings—This citation is correct in Sepkoski 2002.
- Clematocrinus* Jaekel—This citation is correct in Sepkoski 2002.
- Clidochirus* Angelin—FO moved down one substage. Change due to a new species described by Brower (2001) and a new species from Anticosti Island, based on an unpublished manuscript by W.I.A.
- Colpodocrinus* Sprinkle and Kolata—LO moved up five substages with the description of a new species by Donovan (1983).
- Columbicrinus* Ulrich—This citation is correct in Sepkoski 2002.
- Compagicrinus* Jobson and Paul—FO and LO moved down one substage, on the basis of correlations in Smith and Bjerreskov 1994.
- Compsocrinus* Miller—LO moved up two substages because of description of *Compsocrinus relictus* Eckert and Brett (2001) from the Aeronian (Ldov-m) of New York.
- Cornucrinus* Regnéll—FO unresolved but moved up at least two substages, and the LO moved down two substages. *Cornucrinus longicornis* Regnéll has been listed as Late Ordovician to Silurian (Webster 2002), but the Boda Limestone, where it occurs, has been recognized as Rawtheyan (Ash-m) since at least 1971 (see Bergström 1971). The type species, *C. mirus*, was reported from the Middle Ordovician, but its stratigraphic position is uncertain, so its occurrence is not included.
- Cotylacrinna* Brower—This citation is correct in Sepkoski 2002.
- Cremacrinus* Ulrich—FO correct in Sepkoski 2002, but LO unresolved to substage.
- Crineroocrinus* Kolata—This citation is correct in Sepkoski 2002.
- Cryptanisocrinus* Donovan, Doyle, and Harper—This citation is correct in Sepkoski 2002.
- Cupulocrinus* d’Orbigny—This citation is correct in Sepkoski 2002.

SUPPLEMENTAL DATA FOR AUSICH AND PETERS

Ordovician to Llandovery crinoids listed in Sepkoski (2002) Taxon	Range in Sepkoski (2002)			Deviation from Sepkoski ranges to present age assignments (positive indicates Sepkoski [2002] occurrence was too young)			Comments
	FO-P	FO-S	LO-P	LO-S	Lower Limit	Upper Limit	
<i>Abldoglyptocrinus</i>	O	Cara-l	S	Ldov-l	0	5	
<i>Acococrinus</i>	S	Ldov-m	D	Give	ok	Unresolved	
<i>Acolocrinus</i>	O	Cara-l				ok	
<i>Aethocrinus</i>	O	Trem-u	O	Aren-1	-1	-1	
<i>Agostocrinus</i>	O	Cara-l				ok	
<i>Aithrocrinus</i>	O	Ashg-m				ok	
<i>Alisocrinus</i>	O	Ashg-u	S	Wenl	ok	Unresolved	
<i>Allozygocrinus</i>	S	Ldov			Unresolved	Unresolved	
<i>Amarsupioocrinus</i>	S	Ldov	S	Ludl	Unresolved	Unresolved	
<i>Anarchocrinus</i>	O	Cara	O	Ashg-l	-2	0	
<i>Anomalocrinus</i>	O	Cara-l				ok	
<i>Anthracocrinus</i>	O	Cara-l	O	Ashg-m	-4	-6	
<i>Anulocrinus</i>	O	Cara-l				ok	
<i>Apodasmocrinus</i>	O	Cara-l				ok	
<i>Archaeocalyptocrinus</i>	S	Ldov	S	Wenl	Unresolved	Unresolved	
<i>Archaeocrinus</i>	O	Llde	O	Ashg-l	Unresolved	1	
<i>Archaeotaxocrinus</i>	O	Aren-u	O	Llvi-u	0	2	
<i>Atactocrinus</i>	O	Ashg-m				ok	
<i>Atopocrinus</i>	O	Llvi-u			junior synonym		
<i>Atyphocrinus</i>	O	Ashg-l			junior synonym		
<i>Baerocrinus</i>	O	Llvi-l	O	Llde	<i>nomen dubium</i>		
<i>Balacrinus</i>	O	Cara-m				ok	
<i>Bikocrinus</i>	S	Ldov-m				ok	
<i>Bolicrinus</i>	S	Ldov				ok	
<i>Bromidocrinus</i>	O	Cara-l			Unresolved	Unresolved	
<i>Caelocrinus</i>	S	Ldov	S	Ludl	Unresolved, > -1	Unresolved, > -1	not known from Ord-Llandovery
<i>Calceocrinus</i>	O	Cara-l	O	Cara-m	ok	Unresolved	note: genus now in 2 subgenera
<i>Calcidocrinus</i>	O	Llvi-u			1	0	
<i>Canistrocrinus</i>	O	Ashg-m				ok	
<i>Carabocrinus</i>	O	Llde-u	O	Ashg-m	-1	Unresolved	
<i>Carpocrinus</i>	S	Ldov-m	D	Sieg	-1	-1	
<i>Catanaquicrinus</i>	O	Cara-l			-3	-3	
<i>Catatonocrinus</i>	S	Ldov-l				ok	not known from Ord-Llandovery
<i>Celtoocrinus</i>	O	Aren-l				ok	
<i>Chitocrinus</i>	S	Ldov	S	Wenl	Unresolved, > 2	Unresolved	
<i>Cincinnatiocrinus</i>	O	Cara-m	O	Ashg-m		ok	
<i>Clawitullacrinus</i>	O	Ashg-m				ok	
<i>Cleioocrinus</i>	O	Llde-u	O	Cara-m	0	ok	
<i>Clematocrinus</i>	S	Ldov-m	S	Ludl-l		ok	

SUPPLEMENTAL DATA FOR AUSICH AND PETERS (Continued)

Ordovician to Llandovery crinoids listed in Sepkoski (2002) Taxon	Range in Sepkoski (2002)			Deviation from Sepkoski ranges to present age assignments (positive indicates Sepkoski [2002] occurrence was too young)			Comments
	FO:P	FO:S	LO:P	LO:S	Lower Limit	Upper Limit	
<i>Cladochirus</i>	O	Ash-u	M	Tourn-u	1		0
<i>Colpodecrinus</i>	O	Cara-l			0		-5
<i>Columbicrinus</i>	O	Cra-l				ok	
<i>Compagocrinus</i>	O	Aren-u			1		1
<i>Compsocrinus</i>	O	Ashg-m	O	Ashg-u	0		-2
<i>Cornucrinus</i>	O	Cara	S	Ldov-l	Unresolved, > -2		2
<i>Cotylacrinna</i>	O	Cara-m				ok	
<i>Cremacrurus</i>	O	Cara-l	S	Ludl	ok		Unresolved
<i>Crineroocrinus</i>	O	Cara-l				ok	
<i>Cryptoamisosocrinus</i>	O	Ldov-u				ok	
<i>Cupuloocrinus</i>	O	Cara-l	O	Ashg-m			ok
<i>Daedalocrinus</i>	O	Cara-m				ok	
<i>Deltacrinus</i>	S	Ldov	D	Fame-l	junior synonym		
<i>Dendroocrinus</i>	O	Cara-l	S	Ludl	ok		Unresolved
<i>Deocrinus</i>	O	Llvi-u			-2		-2
<i>Diaboloocrinus</i>	O	Llde	O	Ashg-m	Unresolved, > -1		0
<i>Diaphorocrinus</i>	S	Ldov			Unresolved		Unresolved
<i>Difficilicrinus</i>	O	Cara-l				ok	
<i>Dimerocrinites</i>	S	Ldov-u	D	Eife	1		Unresolved
<i>Dolicoocrinus</i>	O	Cara-l				ok	
<i>Drymoocrinus</i>	O	Cara-u	O	Ashg-l			
<i>Dystactocrinus</i>	O	Craa-u	O	Ashg-l	junior synonym		
<i>Ectocrinus</i>	O	Cara-l	O	Ashg-m			0
<i>Elpasocrinus</i>	O	Aren-l			-1		
<i>Eociceroocrinus</i>	O	Ashg-m				ok	
<i>Eomyelodaactylus</i>	S	Ldov-l	S	Ldov-u	2		-1
<i>Eoparisocrinus</i>	O	Cara-m	S	Wnel	0		Unresolved, > 2
<i>Eopatelliocrinus</i>	O	Cara-m	S	Wenl-l	0		> 4
<i>Eopinocrinus</i>	O	Cara-l				ok	
<i>Esthonoocrinus</i>	O	Cara-l			0		-1
<i>Eucalyptocrinites</i>	S	Ldov	D	Eife	Unresolved		Unresolved
<i>Euptychocrinus</i>	O	Cara-m	S	Ldov	0		Unresolved
<i>Eusproocrinus</i>	S	Ldov	S	Ludl	Unresolved, > 2		Unresolved
<i>Eustenocrinus</i>	O	Cara-m				ok	
<i>Gauroocrinus</i>	O	Ashg-m				ok	
<i>Genoocrinus</i>	O	Cara-l	O	Cara-m	0		1
<i>Glaucocrinus</i>	O	Cara-m				ok	
<i>Glyptocrinus</i>	O	Cara-m	S	Ludl	0		Unresolved, > 5

SUPPLEMENTAL DATA FOR AUSICH AND PETERS (Continued)

Ordovician to Llandovery crinoids listed in Sepkoski (2002) Taxon	Range in Sepkoski (2002)			Deviation from Sepkoski ranges to present age assignments (positive indicates Sepkoski [2002] occurrence was too young)			Comments
	FO-P	FO-S	LO-P	LO-S	Lower Limit	Upper Limit	
<i>Grenprisia</i>	O	Cara-m					
<i>Gustabilicrinus</i>	O	Cara-l				ok	
<i>Hagnocrinus</i>	S	Ldov-u	S	Ludl-u		ok	
<i>Hemistreptocrinus</i>	O	Llvi			<i>nomen dubium</i>	ok	
<i>Hercocrinus</i>	O	Llde-u					
<i>Herpetocrinus</i>	S	Ldov-u	S	Ludl	junior synonym		
<i>Heterocrinus</i>	O	Cara-l	O	Cara-u	junior synonym		
<i>Homocrinus</i>	S	Ldov	S	Wen-l	Unresolved		
<i>Hoplocrinus</i>	O	Aren-u	O	Cara	0	Unresolved	0
<i>Hyboecystites</i>	O	Aren-l	O	Cara-m	0		-1
<i>Ibanoocrinus</i>	S	Ldov-m				ok	
<i>Ibexocrinus</i>	O	Aren-u	O	Llvi-u	0	ok	2
<i>Illemtocrinus</i>	O	Cara-m				ok	
<i>Ingocrinus</i>	O	Aren-l	O	Ashg-m	-2	ok	0
<i>Iocrinus</i>	O	Aren-l	O	Cara-m		ok	
<i>Isotomocrinus</i>	S	Ldov-m				ok	
<i>Kanabinoocrinus</i>	S	Ldov			Unresolved		Unresolved
<i>Krimocrinus</i>	S	Ldov			Unresolved		Unresolved
<i>Kylloxocrinus</i>	S	Ldov-m				ok	
<i>Kyroocrinus</i>	S	Ldov-m					
<i>Lampteroocrinus</i>	S	Ldov	S	Ludl	Unresolved		Unresolved
<i>Lecanoocrinus</i>	S	Ldov-u	D	Emsi	0		Unresolved
<i>Luxocrinus</i>	S	Ldov	S	Ludl	Unresolved		Unresolved
<i>Lyonocrinus</i>	S	Ldov			junior synonym		Unresolved
<i>Macuananatyclus</i>	S	Ldov-u	D	Emsi	0		Unresolved
<i>Macrostylocrinus</i>	O	Ashg-m			-1		-1
<i>Maennilicrinus</i>	O	Aren-l			0		-1
<i>Mantiacrinus</i>	S	Ldov-m			-1		-1
<i>Maquoketocrinus</i>	O	Ashg-l					
<i>Meroocrinus</i>	O	Llde	O	Cara-u	Unresolved		Unresolved
<i>Metabolocrinus</i>	O	m			junior synonym		
<i>Mitroocrinus</i>	O	Cara-l					
<i>Musocrinus</i>	O	Ashg-u					
<i>Myelodactylus</i>	S	Ldov-u	D	Give-l	1		0
<i>Neoarchoocrinus</i>	O	Cara-m	D	Gedi	3		Unresolved
<i>Nexocrinus</i>	S	Ldov			Unresolved		Unresolved, > -1
<i>Nonparactocrinus</i>	O	Llvi			<i>nomen dubium</i>		

not known from Ord-Llandovery
A column, not a crown

SUPPLEMENTAL DATA FOR AUSICH AND PETERS (Continued)

Ordovician to Llandovery crinoids listed in Sepkoski (2002) Taxon	Range in Sepkoski (2002)			Deviation from Sepkoski ranges to present age assignments (positive indicates Sepkoski [2002] occurrence was too young)			Comments
	FOLP	FOLS	LO-P	LO-S	Lower Limit	Upper Limit	
<i>Ohioocrinus</i>	O	Cara-m	O	Ashg-l	ok		
<i>Ontariocrinus</i>	O	Cara-m			<i>nomen dubium</i>		
<i>Othneiocrinus</i>	O	Llvi-l			1	1	
<i>Ottawaocrinus</i>	O	Cara-m			ok		
<i>Paideroocrinus</i>	S	Ldov-m			ok		
<i>Palaeocrinus</i>	O	Llde-u	O	Cara-m	ok		
<i>Pandoracrinus</i>	O	Llde			Unresolved	Unresolved	
<i>Paracremacrinus</i>	O	Cara-l			ok		
<i>Paractocrinus</i>	O	Llvi			<i>nomen dubium</i>		
<i>Paradiabolocrinus</i>	O	Cara-l			ok		
<i>Parachaeocrinus</i>	O	Cara-l	O	Ashg-m	0	4	
<i>Parioocrinus</i>	S	Ldov-l			0	-1	
<i>Pararthocrinus</i>	O	Llvi			<i>nomen dubium</i>		
<i>Pateilloocrinus</i>	S	Ldov-m	S	Wenl	0	Unresolved	
<i>Peltacrinus</i>	O	Cara-l			ok		
<i>Penicillocrinus</i>	O	Cara-l			ok		
<i>Peniculocrinus</i>	O	Cara-l			0	-1	
<i>Periglyptocrinus</i>	O	Cara-m	O	Cara-u	0	1	
<i>Perrhocrinus</i>	O	Aren-u			0	-1	
<i>Petalocrinus</i>	S	Ldov-m	S	Wenl	-1	Unresolved	
<i>Phrygiocrinus</i>	S	Ldov-m			ok		
<i>Pisocrinus</i>	S	Ldov-u	D	Eife	2	Unresolved	
<i>Plicodendrocrinus</i>	O	cara-m	O	Ashg-u	ok		
<i>Pogoniptocrinus</i>	O	Aren-l			ok		
<i>Polycrinus</i>	O	Cara-u	O	Ashg-m	ok		
<i>Porocrinus</i>	O	Cara-l	O	Ashg-m	ok		
<i>Praecipulocrinus</i>	O	Cara-m	O	Ashg-m	ok		
<i>Pregazocrinus</i>	S	Ldov			0	3	
<i>Premanicrinus</i>	S	Ldov-u	S	Wen-l	Unresolved	Unresolved	
<i>Proanisocrinus</i>	O	Ashg-m			ok		
<i>Proxenoocrinus</i>	O	Aren-l			ok		
<i>Protaxocrinus</i>	O	Cara-m	D	Gedi	0	Unresolved	
<i>Ptychocrinus</i>	O	Ashg-m	S	Ldov-u	2	0	
<i>Putilovocrinus</i>	O	Aren-l			-1	-1	
<i>Pycnocrinus</i>	O	Cara-m	O	Ashg-m	0	1	
<i>Quinquecaudex</i>	O	Cara-l	O	Ashg-l			
<i>Rasfacrinus</i> [sic]	O	Cara-u?	O	Ashg-l?	1	1	
<i>Ramseyocrinus</i>	O	Aren-l	O	Llvi-l	0	-1	

SUPPLEMENTAL DATA FOR AUSICH AND PETERS (Continued)

Ordovician to Llandovery crinoids listed in Sepkoski (2002) Taxon	Range in Sepkoski (2002)			Deviation from Sepkoski ranges to present age assignments (positive indicates Sepkoski [2002] occurrence was too young)		Comments
	FO-P	FO-S	LO-P	LO-S	Lower Limit	
<i>Reteocrinus</i>	O	Cara-l	O	Ash-m	Unresolved	ok
<i>Revalocrinus</i>	O	Livi?			Unresolved	Unresolved
<i>Rhachicrinus</i>	S	Ldov-m				ok
<i>Rhaphanocrinus</i>	O	Lide-u	O	Ashg-m		ok
<i>Rheocrinus</i>	O	Ashg			Unresolved	Unresolved
<i>Ristnacrus</i>	O	Livi-u	O	Ashg-u	-2	1
<i>Schizocrinus</i>	O	Cara-m			1	0
<i>Serendipocrinus</i>	O	Ashg			Unresolved	Unresolved
<i>Silfonocrinus</i>	S	Ldov-m				ok
<i>Simplococrinus</i>	O	Cara-u			Unresolved	Unresolved
<i>Simopetalocrinus</i>	S	Ldov			Unresolved	ok
<i>Spirocrinus</i>	S	Ldov-m				ok
<i>Stereosaster</i>	S	Ldov-m				ok
<i>Stibarocrinus</i>	S	Ldov-m				ok
<i>Stipatoocrinus</i>	S	Ldov			Unresolved	Unresolved
<i>Sygcauloocrinus</i>	O	Ashg-l	O	Ashg-m	-1	0
<i>Synchiroocrinus</i>	S	Ldov	D	Give	Unresolved, > -1	Unresolved
<i>Tetractonocrinus</i>	O	Aren-u			0	-1
<i>Tetractocrinus</i>	O	Aren-u			<i>nomen dubium</i>	
<i>Tetragonocrinus</i>	O	AREN-l	O	Livi-l		ok
<i>Theleproktocrinus</i>	S	Ldov			Unresolved	Unresolved
<i>Thomasocrinus</i>	S	Ldov			Unresolved	Unresolved
<i>Tirocrinus</i>	S	Ldov-m				ok
<i>Tornatilitrinus</i>	O	Cara-l			junior synonym	
<i>Traskocrinus</i>	O	Cara-l				ok
<i>Triboloporus</i>	O	Cara-l				ok
<i>Trichinocrinus</i>	O	Livi-u			1	1
<i>Tripatoocrinus</i>	O	Livi-l				ok
<i>Trochocrinitis</i>	O	Cara			<i>nomen dubium</i>	
<i>Trypheroocrinus</i>	S	Ldov-m				ok
<i>Tryssocrinus</i>	O	Cara-l				ok
<i>Tunguskocrinus</i>	O	Cara			Unresolved, > -1	Unresolved
<i>Turbocrinus</i>	S	Ldov-m				ok
<i>Typanocrinus</i>	S	Ldov-m				ok
<i>Virucrinus</i>	O	Lide	O	Cara-m	Unresolved, > -1	0
<i>Vosekocrinus</i>	O	Livi-l			1	-1

Younger than Llandovery

SUPPLEMENTAL DATA FOR AUSICH AND PETERS (Continued)

Ordovician to Llandovery crinoids listed in Sepkoski (2002) Taxon	Range in Sepkoski (2002)			Deviation from Sepkoski ranges to present age assignments (positive indicates Sepkoski [2002] occurrence was too young)			Comments
	FO.P	FO.S	LO.P	LO.S	Lower Limit	Upper Limit	
<i>Westheadocrinus</i>	O	Ashg-m	S	Wen-l		ok	
<i>Wilsonocrinus</i>	O	Cara-l	O	Ashg-u	0	ok	-1
<i>Xenocrinus</i>	S	Ldov-m	S	Ldov-m		ok	
<i>Ziocrinus</i>	S	Ldov-m	S	Ldov-m		ok	
Not in Sepkoski (2002) Listing but should have been included							
<i>Catanactocrinus</i>							
<i>Praecursorocrinus</i>							
Cited in Sepkoski (2002) but not cited from Ordovician to Llandovery Interval as now recognized							
<i>Abacocrinus</i>	S	Wen-l	S	Ludl	Unresolved, >1		Unresolved
<i>Alloocrinus</i>	S	Wen-l	D	Give	1		Unresolved
<i>Botryocrinus</i>	S	Wen-l	D	I	2		Unresolved
<i>Calliocrinus</i>	S	Wen-l	S	Ludl	4		Unresolved
<i>Charactocrinus</i>	S	Wen-l	C	Vise-u	2		0
<i>Crotabocrinites</i>	D	Emsi-u	D		14		Unresolved
<i>Culicocrinus</i>	S	Wen-l	D				
<i>Cyathocrinites</i>	S	Wen-l	D	Eife	1		0
<i>Cyrtocrinus</i>	S	Wen-l	D	Fras-u	Unresolved, >3		Unresolved
<i>Eohalysiocrinus</i>	S	Wen-l	D	Sieg	Unresolved, >5		Unresolved
<i>Grypocrinus</i>	D	Emsi-l	D		10		0
<i>Hapalocrinus</i>	S	Wen-l	D		>1		Unresolved
<i>Hirneocrinus</i>	S	Wen-l	D		1		Unresolved
<i>Ichthyocrinus</i>	S	Gedi	D	Fras-u	Unresolved, >1		0
<i>Lyriocrinus</i>	D	Wen-l	D	Emsi-u	Unresolved, >1		0
<i>Melocrinites</i>	S	Wen-l	S	Ludl-l	2		0
<i>Paraptocrinus</i>	S	Wen-l	S	Ludl-l	2		0
<i>Periechocrinus</i>	S	Wen-l	S	Ludl-l	1		0
<i>Siphonocrinus</i>	S	Wen-l	S	Ludl	Unresolved, >1		Unresolved
<i>Thalamocrinus</i>	S	Wen-l	S	Ludl	Unresolved, >1		Unresolved
<i>Zophocrinus</i>	S	Wen-l	S	Ludl	Unresolved, >1		Unresolved

OK but now split into new genera