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Improved confidence intervals for estimating the position of a mass extinction boundary

Steve C. Wang and Charles R. Marshall

Abstract.—Marshall (1995) used the distribution of the endpoints of 50% range extensions added to the stratigraphic ranges of individual taxa to bracket the position of an extinction boundary. Here we describe two improvements to Marshall's method. First, we show that more precise estimates of the position of such a boundary may be obtained using range extensions with confidence levels of less than 50% (e.g., 20%). Second, we introduce a new method of calculating confidence intervals that explicitly takes into account the position of the highest fossil find. Incorporating these improvements leads to confidence intervals for simulated data sets that are approximately four times more precise than those obtained by using Marshall's (1995) original method and approximately twice as precise as those using other published methods. We provide a look-up table that shows for different numbers of taxa the confidence level that should be used to maximize the precision of the estimated position of the extinction boundary, while ensuring that the boundary still lies within the stratigraphic interval bounded by at least one range extension. Unlike some other methods, our method is nonparametric and does not make the restrictive assumption of uniform preservation and recovery potential. We apply the method to Macellari's (1986) ammonite data from the late Cretaceous of Seymour Island, Antarctica.

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Introduction

When a collection of taxa go extinct simultaneously in a mass extinction event, their last occurrences in the fossil record may nonetheless appear gradual because of the incompleteness of the fossil record (Signor and Lipps 1982). Several methods have been proposed to estimate the stratigraphic position of a simultaneous mass extinction boundary, taking into account this incompleteness (Springer 1990; Marshall 1995; Solow 1996; Solow and Smith 2000). Here we build on Marshall's (1995) approach, a nonparametric method for establishing confidence intervals on the position of a hypothesized mass extinction boundary. Using Strauss and Sadler's method (1989) for calculating a range extension on the observed stratigraphic range of a single taxon, Marshall (1995) used information from multiple taxa to arrive at a confidence interval for their common extinction time. In this paper, we propose two improvements on Marshall's method that yield more precise estimates of the position of a mass extinction boundary. First, we propose the use of shorter range extensions (i.e., those having lower confidence levels) in calculating confidence intervals. Second, we propose an alternative method of calculating confidence intervals, which explicitly takes into account the fact that the extinction boundary must lie above the highest fossil find. Our method is nonparametric and does not depend on the restrictive assumption of uniform preservation and recovery potential. We compare our improved confidence intervals with existing methods, whose precision has not previously been evaluated systematically, and show that our improved confidence intervals are one-fourth the width of intervals calculated by using the original Marshall (1995) method, and approximately one-half the width of those using Springer (1990) and Solow (1996). We apply our methods to Macellari's (1986) end-Cretaceous ammonite data from Seymour Island, Antarctica, and show that the estimated position of the extinction boundary is consistent with an iridium anomaly reported by Elliot et al. (1994).

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Range Extensions and Confidence Intervals

We begin by reviewing Marshall's (1995) method. Given an individual taxon i, Marshall (1995) first calculates a C% confidence interval for the upper limit of the taxon's true range. This confidence interval has the form of a range extension added to the position of the highest fossil find for that taxon, with its height $r_{C,i}$ given by Strauss and Sadler's (1989) equation (20):

$$r_{C,i} = [(1 - C)^{-1/(H-1)} - 1]R$$

Here C denotes the desired confidence level (expressed as a decimal between 0 and 1), H the number of fossil horizons, and R the observed stratigraphic range.

(Note that we use the term ''confidence interval'' to refer both to an estimate of the extinction time for a single taxon, and to an estimate of a common extinction time for multiple taxa. The intended meaning in any particular case should be clear from the context. Generally, we will refer to a confidence interval for the stratigraphic range of an individual taxon as a ''C% range extension.'' For example, the terminology ''50% range extension'' should be understood to mean ''the extension above the highest fossil horizon given by a 50% confidence interval for the endpoint of the taxon's true range.'' When estimating the position of a mass extinction boundary affecting multiple taxa, we will use the term ''confidence interval on the position of the mass extinction boundary.'')

The Strauss and Sadler (1989) equation requires that fossil horizons be distributed independently and uniformly throughout the taxon's stratigraphic range, with sampling being continuous. When these assumptions are not satisfied, as is often the case, less restrictive methods of calculating confidence intervals for individual taxa can be applied (Marshall 1994, 1997; Solow 2003). For example, Marshall (1997) describes a generalized method for calculating confidence intervals for any arbitrary known preservation and recovery function, freeing us from the restrictive assumption of uniformity. Using such a method, we can apply the techniques in this paper to data sets with any known preservation and recovery functions.

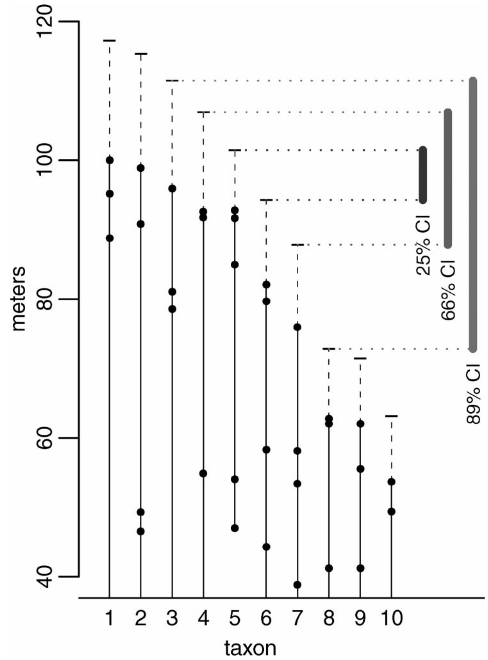

FIGURE 1. Range chart for ten simulated taxa with five fossil horizons each (lower part of ranges omitted for clarity). Vertical bars represent 25% (left), 66% (center), and 89% (right) confidence intervals on the position of the mass extinction boundary, calculated using the original Marshall (1995) method. The 50% range extension for each individual taxon is shown as a vertical dashed line extending above each taxon's stratigraphic range. The position of the true extinction boundary for this simulated data set is at 100 meters.

Formally, let u_i denote the height of the highest fossil horizon found for taxon i, which clearly gives a lower bound on the extinction boundary for that taxon. We can then state with C% confidence that the true extinction boundary lies in the range extension given by the interval $(u_i, u_i + r_{C,i})$. Let $U_{C,i}$ denote the upper endpoint of this range extension; that is, $U_{C,i} = u_i + r_{C,i}$. We calculate such a range extension for each taxon of a collection of n taxa hypothesized to have gone extinct simultaneously in a mass extinction event. These n range extensions are then used to bound a confidence interval for the hypothesized simultaneous extinction boundary of the n taxa.

As a concrete example, imagine $n = 10$ taxa having five fossil horizons each, all of which go extinct simultaneously. Figure 1 shows a range chart for the upper portions of the ranges of ten such taxa. Also shown are 50% range extensions for each taxon; the taxa are sorted from left to right by the tops of their 50% range extensions. For these simulated data, assume that the position of the simultaneous mass extinction boundary is at 100 meters. To apply the methodology of Marshall (1995), we calculate the upper endpoint $U_{50,i}$ of the 50% range extension for each taxon i. Inherent in the construction of a 50% range extension is the property that it contains the true extinction boundary with probability 0.5. (Note that it is only proper to speak of the probability that a range extension includes the true extinction boundary *before* the data have been observed. After the data have been observed, the range extensions are fixed and either do or do not include the true boundary. In this case, we speak of the ''confidence'' that the range extension contains the true boundary.) Conversely, there is a 0.5 probability that the true extinction boundary is not contained in the 50% range extension—in which case it must lie above the range extension.

Given ten taxa, the statistical expectation is that five of the 50% range extensions will contain the true extinction boundary, and the other five will not. That is, we expect that the position of the true extinction boundary will lie below the upper endpoints of five of the 50% range extensions and above the upper endpoints of the other five. In other words, the position of the true extinction boundary is expected to lie between the upper endpoints of the fifth and sixth highest range extensions. This interval constitutes a confidence interval for the position of the true extinction boundary.

To express this idea formally, let $U_C^{(i)}$ denote the ith of the upper endpoints $U_{C,i}$ when sorted from lowest to highest (i.e., the ith order statistic of the $U_{C,i}$) . Let $(U_C^{(i)}, U_C^{(j)})$ denote the interval bounded by the upper endpoints of the ith and jth sorted range extensions. Using this notation, the interval $(U_{50}^{(5)}, U_{50}^{(6)})$ is a confidence interval for the position of the true extinction boundary in the example above, because this interval is the set of all points that are contained within exactly five of the ten range extensions—namely, the five highest range extensions (Fig. 1, left vertical bar).

What is the confidence level of this confidence interval, $(U_{50}^{(5)}, U_{50}^{(6)})$? By definition, the confidence level is equal to the probability that the true extinction boundary lies in the interval $(U_{50}^{(5)}, U_{50}^{(6)})$. To calculate this probability, we use the binomial distribution. Let Y denote the number of range extensions that contain the position of the true extinction boundary. Then, assuming the fossil records of the taxa are independent (conditional on the occurrence of a simultaneous extinction), Y follows a binomial distribution with number of trials $n = 10$ and probability of success $p = 0.5$.

The true extinction boundary lies in the interval $(U_{50}^{(5)}, U_{50}^{(6)})$ if and only if it lies below the upper endpoints of exactly five of the 50% range extensions (Fig. 1, left vertical bar). In other words, exactly five of the 50% range extensions must contain the true extinction boundary, which is to say that $Y = 5$. Because $P(Y = 5) = 0.246$ for $Y \sim \text{binomial}(n = 10, p = 0.5)$, then $(U_{50}^{(5)}, U_{50}^{(6)})$ is a 24.6% confidence interval for the true extinction boundary. Similarly, $(U_{50}^{(4)}, U_{50}^{(7)})$ is a 65.6% confidence interval because $P(Y = 4, 5, \text{or } 6) = 0.205 + 0.246 + 0.205 = 0.656$ (Fig. 1, center vertical bar), and $(U_{50}^{(3)}, U_{50}^{(8)})$ is an 89.1% confidence interval because $P(Y = 3, 4, 5, 6, \text{or } 7) = 0.117 + 0.205 + 0.246 + 0.205 + 0.117 = 0.891$ (Fig. 1, right vertical bar). Confidence intervals based on this approach are used by Marshall (1995, 1998, 2001) and by Marshall and Ward (1996), although these sources do not explicitly describe how the intervals are calculated.

In the following sections, we discuss two improvements that increase the precision of Marshall's (1995) method. First, we use shorter range extensions—that is, C% range extensions with $C < 50\%$. Second, we modify the binomial calculation of the confidence level to explicitly account for the position of the highest fossil find, which must necessarily give a lower bound on the position of the mass extinction boundary. This solves a potential problem with the original Marshall (1995) method, which sometimes predicts that the extinction boundary could lie below the highest fossil find. Together, these improvements allow us to ''pin down'' the extinction boundary with substantially greater precision.

Using Shorter Range Extensions

In this section, we discuss our first improvement on Marshall's (1995) method—the use of

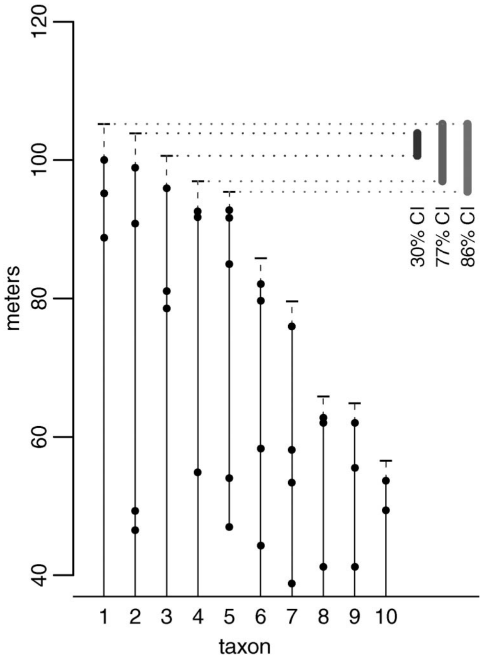

FIGURE 2. Range chart for the same ten simulated taxa shown in Figure 1. Vertical bars represent 30% (left), 77% (center), and 86% (right) confidence intervals on the position of the mass extinction boundary, calculated with our first improvement over Marshall's (1995) method: the use of range extensions with $C < 50\%$. The 20% range extension for each individual taxon is shown as a vertical dashed line extending above each taxon's stratigraphic range. The position of the true extinction boundary for this simulated data set is at 100 meters. Note that these confidence intervals on the position of the mass extinction boundary are narrower than those in Figure 1, resulting in a more precise estimate.

range extensions with values of C less than 50%. This improvement leads to narrower confidence intervals and thus more precise estimates of the position of an extinction boundary.

Instead of using $C = 50\%$, consider an example, shown in Figure 2, using $C = 20\%$, with the same taxa and horizons shown in Figure 1. Each taxon's 20% range extension is shown, and the taxa are sorted from left to right by the tops of their 20% range extensions. (For the sake of expository clarity, this simulated data set was chosen so that the ordering of taxa in Figure 1 would match that of Figure 2.) In this case we expect that 20% (two of ten) of the range extensions will contain the true extinction boundary, and 80% will not. We therefore take the interval $(U_{20}^{(8)}, U_{20}^{(9)})$ as an estimate of the position of the extinction boundary, because it is the set of points contained in exactly two (i.e., the two highest) of the ten 20% range extensions (Fig. 2, left vertical bar). That is, points in this interval are contained within the ninth and tenth highest range extensions, but not within the eight others.

The confidence level associated with this confidence interval can be calculated in a manner similar to that described earlier for intervals using 50% range extensions. As before, let Y denote the number of range extensions that contain the position of the true extinction boundary. Here Y has a binomial distribution with number of trials $n = 10$ and probability of success $p = 0.2$.

The true extinction boundary lies in the interval, $(U_{20}^{(8)}, U_{20}^{(9)})$ if and only if it lies below the upper endpoints of exactly two of the 20% range extensions (Fig. 2, left vertical bar). In other words, exactly two of the 20% range extensions must contain the true extinction boundary, which is to say that $Y = 2$. Because $P(Y = 2) = 0.302$ for $Y \sim \text{binomial}(n = 10, p = 0.2)$, then $(U_{20}^{(8)}, U_{20}^{(9)})$ is a 30.2% confidence interval for the true extinction boundary. Similarly, $(U_{20}^{(7)}, U_{20}^{(10)})$ is a 77.2% confidence interval because $P(Y = 1, 2, \text{ or } 3) = 0.772$ (Fig. 2, center vertical bar), and $(U_{20}^{(6)}, U_{20}^{(10)})$ is an 86.0% confidence interval because $P(Y = 1, 2, 3, \text{ or } 4) = 0.860$ (Fig. 2, right vertical bar). Note that the 30.2%, 77.2%, and 86.0% confidence intervals in Figure 2 are narrower than the approximately corresponding 24.6%, 65.6%, and 89.1% confidence intervals in Figure 1, respectively.

Why are confidence intervals calculated using $C < 50\%$ more precise than those calculated with $C = 50\%$? The height $r_{C,i}$ of a range extension is shorter for smaller values of C; compare the heights of the range extensions in Figures 1 and 2, for instance. (In fact, at the extreme, $C = 0\%$ corresponds to an interval of zero height.) All else being equal, using shorter range extension allows us to locate the position of the extinction boundary more precisely. As the range extensions become shorter, the distances between their upper endpoints become smaller. A shorter distance between two upper endpoints results in a narrower confidence interval, because a confidence interval as defined here is the interval between a pair of upper endpoints. Thus, using $C < 50\%$ allows us to estimate the position of extinction boundaries more precisely than $C = 50\%$. This can be seen in Figures 1 and 2: the 86% confidence interval calculated with $C = 20\%$ (Fig. 2, right vertical bar) is roughly one-fourth the width of the 89% confidence interval calculated using $C = 50\%$ (Fig. 1, right vertical bar), and the 77% confidence interval calculated with $C = 20\%$ is roughly one-half the width of the 66% confidence interval calculated with $C = 50\%$, despite having a higher confidence level. (Note that because of the discreteness in the number of range extensions used, K% confidence intervals can be found only for certain values of K, so that the confidence levels could not be matched exactly.)

Taking into Account the Highest Find

In this section, we discuss our second improvement on Marshall's (1995) method—calculating confidence intervals that explicitly take into account the position of the highest fossil find.

Neither the Marshall (1995) method nor the method described in the previous section explicitly takes into account that the position of the true extinction boundary must lie above u_i (defined previously as the highest fossil find for the ith taxon) for all taxa i. With these methods, it is possible for part of a confidence interval to lie below the highest fossil find, which is clearly problematic. (Neither Springer's [1990] nor Solow's [1996] method has this problem.)

In Figure 1, for instance, notice that parts of the 25%, 66%, and 89% confidence intervals lie below the highest fossil find. In rare cases, it is even possible for the entire confidence interval to lie below the highest fossil find. This possibility stems from Marshall's (1995) original dual-purpose conception of the method. Marshall (1995) initially envisioned the method as (1) a test of the hypothesis of simultaneous extinction and (2) an estimate of the position of the extinction boundary, if the hypothesis of simultaneous extinction is not rejected. If the entire confidence interval lies below the highest find, the hypothesis of simultaneous extinction is rejected, and therefore a confidence interval for the position of a simultaneous extinction boundary is not appropriate.

However, even when the extinction is in fact simultaneous, it is still possible for part or all of the confidence interval to lie below the highest find. This may occur because the original Marshall (1995) method does not use the position of the highest find as the lower bound of the confidence interval. Here we introduce a revised method for calculating confidence intervals that explicitly takes into account this information.

Formally, let u denote the position of the highest fossil find among all n taxa. Recall that $U_C^{(i)}$, as defined previously, denotes the position of the ith highest of the upper endpoints $U_{C,i}$ of the range extensions. Our revised method for calculating confidence intervals always sets the lower endpoint of a confidence interval equal to u, the highest fossil find; this guarantees that no part of the confidence interval lies below the highest fossil find. The upper endpoint of the confidence interval is set to the upper endpoint $U_C^{(i)}$ of the ith highest range extension, with the level of confidence being determined by the value of i chosen.

For example, Figure 3 shows the same taxa and finds as in Figures 1 and 2, with 50% range extensions. Consider the interval (u, $U_{50}^{(10)}$) (Fig. 3, right vertical bar). The probability that the position of the true extinction boundary is contained in this interval is 99.9%. This is calculated as follows: the probability that the position of the true extinction boundary lies *below* this interval is 0% (because the true extinction boundary cannot lie below the highest fossil find, u). The probability that the position of the true extinction boundary lies *above* this interval is 0.1%: the probability that the boundary lies above one 50% range extension is 0.5, so the probability that it lies above all ten 50% range extensions (and therefore the entire interval) is $(0.5)^{10} = 0.001$, or 0.1%. Because the total probability that the position of the true extinction boundary lies outside this interval is $(0\% + 0.1\%) = 0.1\%$, the probability that the interval contains the true extinction boundary must therefore be $(100\% - 0.1\%)$, or 99.9%. Thus the interval

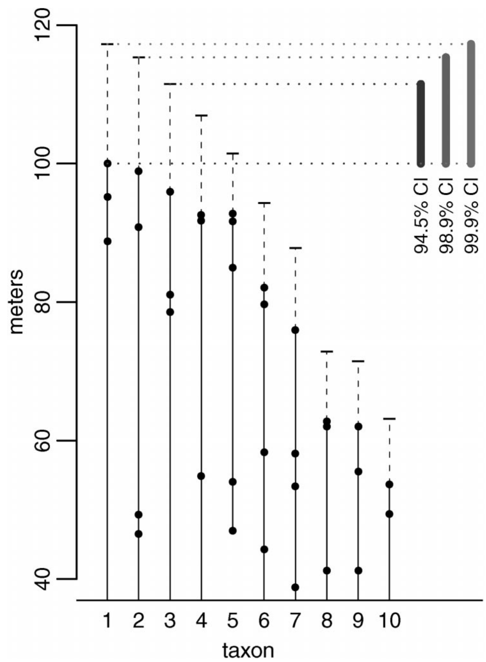

FIGURE 3. Range chart for the same ten simulated taxa shown in Figures 1 and 2. Vertical bars represent 94.5% (left), 98.9% (center), and 99.9% (right) confidence intervals on the position of the mass extinction boundary, calculated with the second improvement over Marshall's (1995) method: taking into account the fact that the position of the mass extinction boundary must lie above the highest fossil find. The 50% range extension for each individual taxon is shown as a vertical dashed line extending above the taxon's stratigraphic range. The position of the true extinction boundary for this simulated data set is at 100 meters.

$(u, U_{50}^{(10)})$ is a 99.9% confidence interval for the position of true extinction boundary.

In general, we define a confidence interval to be an interval of the form $(u, U_C^{(i)})$, for any value of C and i. Because the lower endpoint of the confidence interval is always the position of the highest fossil find, we eliminate the possibility of a confidence interval extending below the highest find. To calculate the confidence level associated with any such interval, we use binomial probabilities in the same manner as described earlier. As an example, we repeat the calculation for the interval $(u, U_{50}^{(10)})$ using binomial probabilities. Let Y denote the number of range extensions that contain the position of the true extinction boundary. In our example above (with $n = 10$ taxa and $C = 50\%$), Y follows a binomial distribution with number of trials $n = 10$ and probability of success $p = 0.5$.

The true extinction boundary lies in the interval $(u, U_{50}^{(10)})$ if and only if it lies below the upper endpoint of the highest range extension. In other words, the true extinction boundary must be contained in at least one (i.e., the highest) of the 50% range extensions, which is to say that $Y \geq 1$. Because $P(Y \geq 1) = 0.999$ for $Y \sim \text{binomial}(n = 10, p = 0.5)$, then $(u, U_{50}^{(10)})$ is a 99.9% confidence interval for the true extinction boundary.

Confidence levels for other intervals can be calculated in a similar manner. For example, what is the confidence level of the interval $(u, U_{50}^{(9)})$? The true extinction boundary lies in the interval $(u, U_{50}^{(9)})$ if and only if it lies below the upper endpoint of the two highest range extensions (Fig. 3, center vertical bar). In other words, the true extinction boundary must be contained in at least two (i.e., the highest two) of the 50% range extensions, which is to say that $Y \geq 2$. Because $P(Y \geq 2) = 0.989$ for $Y \sim \text{binomial}(n = 10, p = 0.5)$, then $(u, U_{50}^{(9)})$ is a 98.9% confidence interval for the true extinction boundary. Similarly, the interval $(u, U_{50}^{(8)})$ is a 94.5% confidence interval because $P(Y \geq 3) = 0.945$ (Fig. 3, left vertical bar), the interval $(u, U_{50}^{(7)})$ is an 82.8% confidence interval because $P(Y \geq 4) = 0.828$ (not shown), and so on.

Notice that the intervals shown in Figure 3 are narrower than the intervals in Figure 1, which were calculated with the original Marshall (1995) method. Moreover, this is true even though the confidence intervals in Figure 3 have much higher confidence levels.

To obtain the greatest improvement in the width of confidence intervals, we incorporate both improvements, using the new calculation method and $C = 20\%$ range extensions. Figure 4 shows the same taxa and finds as in Figures 1–3, with 20% range extensions. Consider the interval $(u, U_{20}^{(10)})$. As described earlier, we use binomial probabilities to calculate the confidence level of this interval.

The true extinction boundary lies in the interval $(u, U_{20}^{(10)})$ if and only if it lies below the upper endpoint of the highest range extension (Fig. 4, right vertical bar). In other words, the true extinction boundary must be contained in at least one (i.e., the highest) of the 20% range extensions, which is to say that $Y \geq 1$. Because $P(Y \geq 1) = 0.893$ for $Y \sim \text{binomial}(n = 10, p$

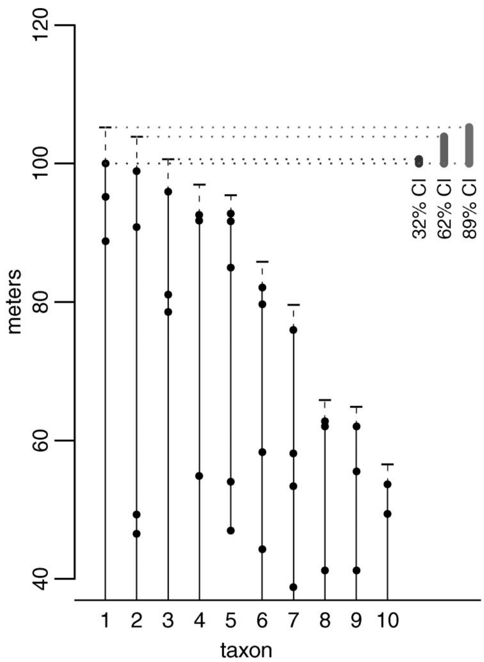

FIGURE 4. Range chart for the same ten simulated taxa shown in Figures 1–3. Vertical bars represent 32% (left), 62% (center), and 89% (right) confidence intervals on the position of the mass extinction boundary, calculated with the new calculation method incorporating both improvements over Marshall's (1995) method. The 20% range extension for each individual taxon is shown as a vertical dashed line extending above the taxon's stratigraphic range. The position of the true extinction boundary for this simulated data set is at 100 meters. These confidence intervals are narrower than those in Figure 1, thus estimating the position of the extinction boundary more precisely.

= 0.2), then (u, $U_{20}^{(10)}$) is an 89.3% confidence interval for the true extinction boundary. Similarly, (u, $U_{20}^{(9)}$) is a 62.4% confidence interval for the true extinction boundary because $P(Y \geq 2) = 0.624$ (Fig. 4, center vertical bar), and (u, $U_{50}^{(8)}$) is a 32.2% confidence interval because $P(Y \geq 3) = 0.322$ (Fig. 4, left vertical bar). Clearly, the 89% interval in Figure 4 is substantially more precise than the 89% interval in Figure 1; in fact, it is approximately one-seventh the width.

Results

In this section we compare the performance of our method with that of existing methods by Springer (1990), Marshall (1995), and Solow (1996), which have never been systematically compared in the literature.

We simulated 1000 data sets of 10 taxa each using the statistics programs R (version 1.6.2) and S-plus (Version 4.5). (See the Table 1 caption for details on the simulation methodology.) Using these simulated data sets, we empirically verified the nominal coverage probabilities of the confidence intervals calculated with our new method (e.g., confirming that the purported 89% confidence intervals in fact contain the position of the true extinction boundary 89% of the time). Table 1 shows the empirical coverage probabilities along with standard errors derived from the binomial distribution. The empirical coverage probabilities are correct within simulation error, demonstrating the correctness of the method. (The nominal coverage probabilities were also verified for the other three methods and found to be correct.)

We also calculated the widths of confidence intervals calculated from the 1000 simulated data sets by using the various methods. Figure 5 displays histograms of the widths of these confidence intervals, and Table 2 gives sum-

TABLE 1. Nominal and empirical coverage probabilities of confidence intervals calculated with the new calculation method (taking into account the position of the highest fossil find). Nominal confidence levels were calculated from the binomial distribution (see examples in text). Empirical coverage probabilities were calculated from a simulation with 1000 data sets, each having ten taxa. The number of fossil horizons for each taxon was randomly generated from a Poisson distribution having mean = 6, constrained to have a minimum of four horizons and a maximum of 30 horizons. The locations of the horizons were then placed randomly according to a uniform distribution. Calculation of standard errors was based on the nominal confidence levels. The empirical probabilities are correct within simulation error; the discrepancy between the nominal and empirical coverage probabilities are all less than one standard error.

	Using 50% range extensions		Using 20% range extensions	
Nominal confidence level	0.828	0.945	0.624	0.893
Empirical coverage probability	0.830	0.940	0.613	0.888
Standard error	0.012	0.007	0.015	0.010

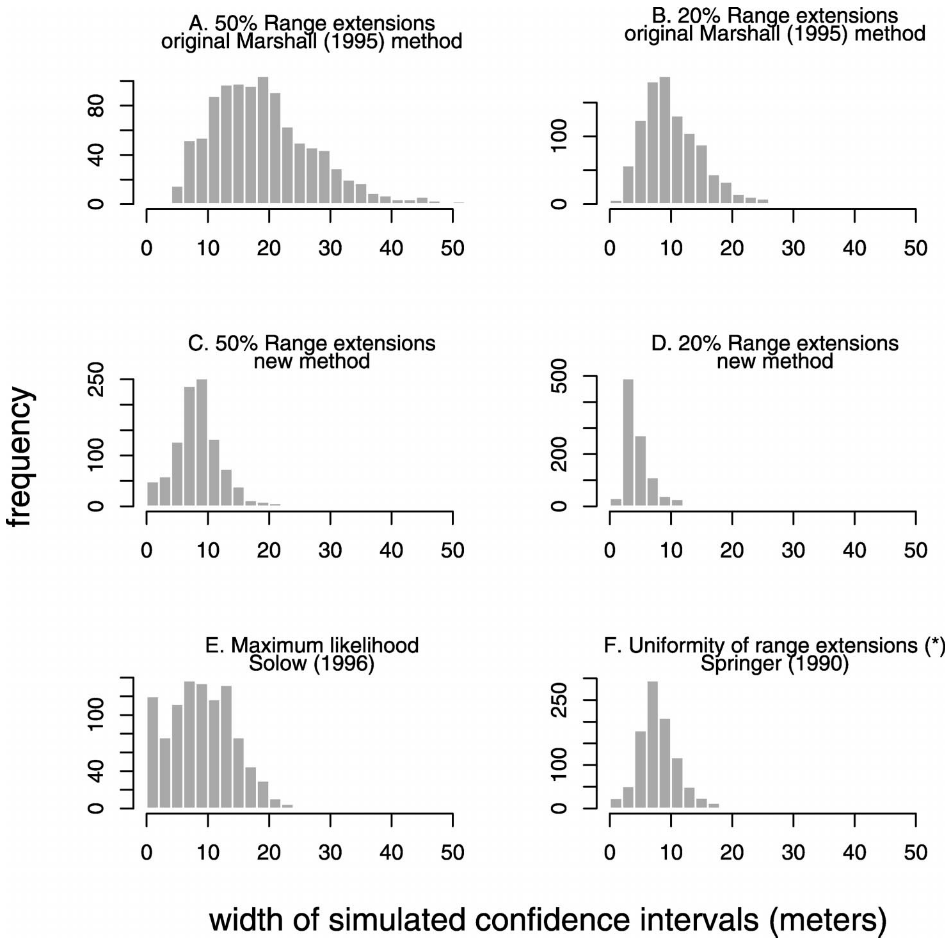

FIGURE 5. Histograms of widths of confidence intervals calculated with the various methods. Each confidence interval width is calculated as (*upper endpoint* − *lower endpoint*). Results were calculated from a simulation with 1000 data sets, each having ten taxa; see Table 1 caption for details on the simulation. Units are given in meters; the position of the true extinction boundary is at 100 meters. The horizontal axis for all panels represents the width of the confidence interval for the mass extinction boundary; the vertical axis represents how often each width occurred in 1000 simulations. (*) See Table 2 caption for details on instances in which the Springer method is unable to calculate an interval.

mary statistics. Figure 6 displays the locations of a randomly chosen subset of 100 of these confidence intervals (only 100 confidence intervals are shown, as showing all 1000 would have made the figure illegible). As can be seen in the tables and figures, our new method achieves a substantial increase in precision compared to existing methods. The widths of confidence intervals calculated by using 20% range extensions and the new calculation method are approximately one-half the width of those calculated by using Springer's (1990) method and Solow's (1996) method, and one-quarter the width of those calculated by using 50% range extensions and the original Marshall (1995) method.

Choosing the Best Value of C.—A natural question is what value of C to choose to maximize the precision of the estimated position of the mass extinction boundary. If smaller values of C give more precise confidence intervals, the logical extreme would be to use $C = 0\%$. But 0% range extensions would have zero width, and none of them would be expected to contain the true extinction boundary. We could thus say only that we are 100% confident that the true extinction boundary lies above the highest fossil horizon—a trivial conclusion

TABLE 2. Summary statistics for widths of confidence intervals calculated with various methods. Results were calculated from a simulation with 1000 data sets, each having ten taxa (all methods used the same simulated data sets). See Table 1 for details on the simulation methodology. Units are given in meters; the true stratigraphic range in the simulation was 100 meters. Because of the discreteness in the number of taxa, confidence levels for various methods match only approximately. (*) denotes a limitation of the Springer (1990) method, which may fail to calculate a confidence interval in some instances. The method calculates confidence intervals by determining the set of points x for which a hypothesis test would not reject the null hypothesis of simultaneous extinction at x. For some data sets, there are no such points—the hypothesis test would reject a simultaneous extinction at *all* points, at the given alpha level. In such a case, no confidence interval can be calculated, and these cases are excluded from the summary statistics in the tables and plots. This occurred in 25 out of 1000 simulated data sets. These are data sets in which the other methods would be expected to yield wider-than-average confidence intervals because of the variability of the highest fossil horizons, which may artificially favor the Springer method in this comparison.

Method	Confidence level	Lower quartile	Median	Mean	Upper quartile
A. 50% range extensions, original Marshall (1995) calculation method	89%	12.98	17.96	19.00	23.73
B. 20% range extensions, original Marshall (1995) calculation method	86%	6.73	9.34	10.26	13.10
C. 50% range extensions, new calculation method	95%	6.12	8.25	8.36	10.34
D. 20% range extensions, new calculation method	89%	3.03	3.89	4.76	5.37
E. Maximum likelihood, Solow (1996)	89%	5.10	8.80	9.02	12.80
F. Uniformity of range extensions, Springer (1990)	89%	5.94 (*)	7.62 (*)	8.01 (*)	9.61 (*)

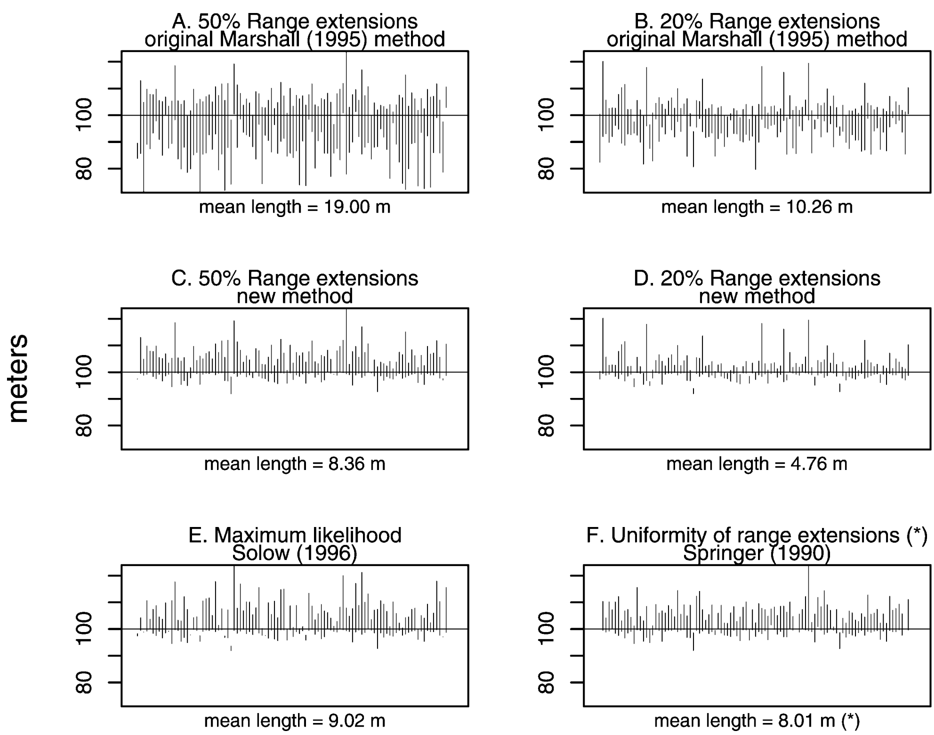

FIGURE 6. Locations of 100 confidence intervals calculated with the various methods. Results were calculated from a simulation with 1000 data sets, each having ten taxa; see Table 1 caption for details. To preserve legibility, results from only 100 of the 1000 simulated data sets are shown. Units are given in meters; the position of the true extinction boundary is at 100 meters (indicated by horizontal line). Note that for all methods except the original Marshall (1995) method, confidence intervals on the position of the mass extinction boundary extend further above the extinction boundary than below it. This lack of symmetry results from the fact that the true extinction boundary is constrained below by the location of the highest fossil horizon, but is unconstrained above. (*) See Table 2 caption for details on instances in which the Springer method is unable to calculate an interval.

because this condition is obviously a necessary constraint.

Practical guidelines for choosing C are needed. Although smaller values of C may seem optimal, in practice there are two rules that limit how small a value of C we can choose. The first rule is that for n taxa, we must choose a value of C that is a multiple of $1/n$. For instance, if $n = 10$ taxa, only values of C that are multiples of 1/10 (i.e., multiples of 10%) are possible. That is, we are limited by the discreteness imposed by values of n, the number of taxa.

The second rule is that we must choose a value of C large enough to achieve the desired level of confidence on the position of the extinction boundary. This second rule is important because choosing overly small values of C makes it impossible to achieve intervals with high confidence levels. For example, consider a data set with $n = 10$ taxa using $C = 10\%$. The widest possible confidence interval that can be constructed with our method is $(u, U_{10}^{(10)})$, extending from the highest fossil find to the upper endpoint of the highest range extension (Fig. 7, vertical bar). Even though this is the widest possible confidence interval, it achieves a confidence level of only 65%. This is calculated as follows: the probability that the position of the true extinction boundary lies *below* this interval is 0% (because the true extinction boundary cannot lie below the highest fossil find, u). The probability that the position of the true extinction boundary lies *above* this interval is 35%. (The probability that the boundary lies above one 10% range extension is 0.9, so the probability that it lies above all ten 10% range extensions is $(0.9)^{10} = 0.35$, or 35%.) Because the total probability that the position of the true extinction boundary lies outside this interval is (0% + 35%) = 35%, the probability that the interval contains the true extinction boundary must therefore be (100% − 35%), or 65%. Thus the interval $(u, U_{10}^{(10)})$ is a 65% confidence interval for the position of true extinction boundary.

Because wider intervals have higher confidence levels, and this is the widest possible interval that can be constructed under these conditions, it is therefore not possible to exceed 65% confidence using $C = 10\%$ range extensions. If we desire a higher confidence level, then, we must choose $C > 10\%$.

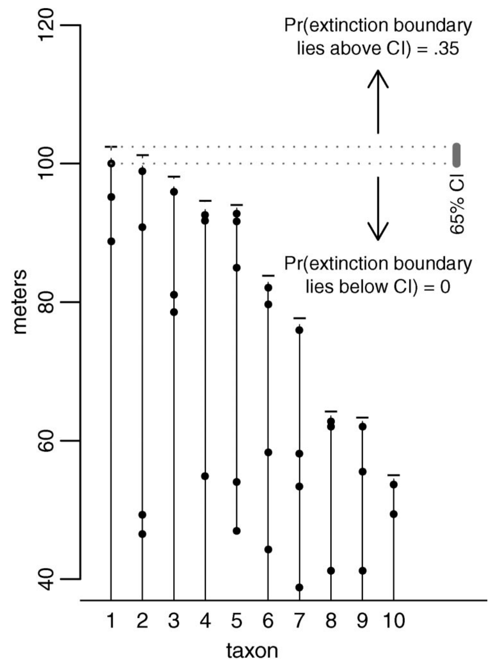

FIGURE 7. Range chart for the same ten simulated taxa shown in Figures 1–4. Using 10% range extensions, the widest possible confidence interval calculated with the new calculation method (vertical bar at right) achieves a confidence level of only 65%. Higher confidence levels cannot be achieved by using $C = 10\%$ range extensions. The maximum confidence level is limited by the fact that there is a 35% probability that the position of the true extinction boundary lies above all ten 10% range extensions. (Because the boundary lies above any one 10% range extension with probability = 0.9, it lies above all ten 10% range extensions with probability $(0.9)^{10} = 0.35$, or 35%.)

In general, the highest confidence level achievable is limited by the probability that the position of the true extinction boundary lies above the upper endpoint of all range extensions. To be precise, let Y denote the number of C% range extensions that contain the position of the true extinction boundary. Then Y follows a binomial distribution with number of trials n and probability of success $p = C$ (here expressed as a decimal between 0 and 1). The highest confidence level that can be achieved by using C% range extensions is equal to $1 - P(Y = 0)$. We must therefore choose a value of C for which $P(Y = 0)$ is sufficiently small, so that the confidence level $1 - P(Y = 0)$ will be acceptably large. For $n = 10$ taxa, suppose we want a 95% confidence

TABLE 3. Recommended values for choosing C to maximize the precision of estimates of the position of mass extinction boundaries. C is the confidence level used in confidence intervals on the stratigraphic ranges of individual taxa. For the given number of taxa, the table gives the smallest value of C needed to achieve 90%, 95%, and 99% confidence intervals on the position of the extinction boundary, according to criteria given in the text.

No. of taxa	Min. C needed to achieve 90% confidence	Min. C needed to achieve 95% confidence	Min. C needed to achieve 99% confidence
3	67%	67%	—
4	50%	75%	75%
5	40%	60%	60%
6	33%	50%	67%
7	29%	43%	57%
8	25%	38%	50%
9	22%	33%	44%
10	30%	30%	40%
11	27%	27%	36%
12	25%	25%	33%
13	23%	23%	31%
14	21%	21%	29%
15	20%	20%	27%
16	19%	19%	25%
17	18%	18%	24%
18	17%	17%	22%
19	16%	16%	21%
20	15%	15%	20%
25	12%	12%	16%
30	10%	10%	13%
35	9%	9%	11%
40	8%	8%	10%
45	7%	7%	11%
50	6%	6%	10%

interval. We might then consider $C = 20\%$ and $C = 30\%$ (because we saw above that $C = 10\%$ could not achieve a confidence level of 95%). Using $C = 20\%$, we are able to achieve a confidence level of at most 89%, because $P(Y = 0) = 0.11$ for $Y \sim \text{binomial}(n = 10, p = 0.2)$, and $1 - 0.11 = 0.89$, or 89%. But using $C = 30\%$, we are able to achieve a confidence level of 97%, because $P(Y = 0) = 0.03$ for $Y \sim \text{binomial}(n = 10, p = 0.3)$, and $1 - 0.03 = 0.97$, or 97%. Thus we choose $C = 30\%$ so we can achieve the desired confidence level of 95% (or better) for the position of the extinction boundary.

Table 3 below gives the smallest values of C (for selected values of n) that are needed to achieve 90%, 95%, and 99% confidence intervals on the position of a mass extinction boundary. Calculations of these values took into account the above two rules. In summary, we propose that one choose the smallest possible value of C that will achieve the desired level of confidence for the confidence interval on the position of the extinction boundary.

Note that the values in Table 3 should be taken as general guidelines rather than strict prescriptions. In our examples above, we used $C = 20\%$ rather than $C = 30\%$ with ten taxa, whereas the table recommends using a minimum of $C = 30\%$ to achieve 90% confidence. However, with $C = 20\%$ we were able to achieve a maximum confidence level of 89%. This is close enough to 90% that we prefer the gain in precision afforded by using $C = 20\%$ over the negligible gain in confidence, assuming a confidence of approximately 90% is acceptable to us.

We also note that it is possible to achieve higher levels of confidence with small numbers of taxa by modifying the method slightly, using values of $C > 50\%$. For instance, suppose we have three taxa. Using the method as described, we can achieve a 96% confidence interval by using $C = 66.6\%$, because there is a 0.04 probability that the true extinction boundary lies above all three range extensions (because $P(Y = 0) = 0.04$ for $Y \sim \text{binomial}(n = 3, p = 0.666)$). However, the discreteness of our approach is a difficulty if we want to calculate a 99% confidence interval and have only three taxa. Using the binomial approach, we would use 76% range extensions for each taxon to achieve 99% confidence. There would then be a 0.01 probability that the true extinction boundary lies above all three range extensions (because $P(Y = 0) = 0.01$ for $Y \sim \text{binomial}(n = 3, p = 0.76)$). However, with three taxa, the discreteness makes it difficult to determine an interval above which we expect 76% of the range extensions to lie. That is, with 76% range extensions, the extinction boundary would be expected to lie below $(3)(1 - 0.76) = 0.72$ of the upper endpoints, which is not a whole number and does not give us a feasible confidence interval.

The Seymour Island Ammonites.—We apply our method to a data set of ammonites collected by Macellari (1986) from the late Cretaceous of Seymour Island, Antarctica. Macellari's data set satisfies the assumptions of independence and uniformity required by the

Strauss and Sadler confidence intervals method (Springer 1990), and it was collected systematically and without regard for testing extinction-time hypotheses. The data used here are from the ten ammonite species with at least one fossil horizon reported by Macellari in the upper 300 meters of the Cretaceous on Seymour Island. Because Macellari (1986) does not give the numerical values of the horizon locations, the values used here were estimated by hand from Macellari's Figure 6 and are the same as those used by Marshall (1995). A substantial iridium anomaly was reported by Elliot et al. (1994) ten meters above Macellari's last ammonite specimen, providing an independent estimate of the Cretaceous/Tertiary boundary. The last specimens of the ten ammonite species are distributed over a range of roughly 10–60 meters below the iridium anomaly.

Marshall (1995) found the disappearance of ammonite species from this site to be consistent with simultaneous extinction, and he estimated the extinction boundary at 7–11 meters above Macellari's last ammonite find. Using confidence level ≈ 0.95, Marshall estimated the extinction boundary at 0–20 meters above Macellari's last ammonite.

Solow (1996) also found the disappearance of ammonite species from this site to be consistent with simultaneous extinction. Using confidence level 0.95, Solow estimated the extinction boundary at 0–13 meters above Macellari's last ammonite.

Springer (1990) also found the disappearance of ammonite species from this site to be consistent with simultaneous extinction, estimating the extinction boundary at 8 meters above Macellari's last ammonite. Using confidence level 0.95, Springer estimated the extinction boundary at 0–25 meters above Macellari's last ammonite. Thus Marshall's, Solow's, and Springer's conclusions agree with each other and the observed iridium anomaly of Elliot et al., although the widths of the 95% confidence intervals vary.

Figure 8A shows the upper portions of the stratigraphic ranges of Macellari's ten ammonite species and their fossil horizons, with an 89% confidence interval calculated by using $C = 50\%$ range extensions and the original Marshall (1995) calculation method. Figure 8B shows the same data with an 89% confidence interval calculated by using $C = 20\%$ range extensions and the new calculation method. The latter interval is approximately one-third the width of the former. Table 4 presents confidence intervals calculated by using the various methods. The confidence intervals using 20% range extensions and the new calculation method are substantially narrower than those calculated with the other methods, giving us a more precise estimate of the extinction boundary. (Note that the values in Table 4 differ slightly from those reported by Solow [1996] and Springer [1990] respectively. These differences are due to differences in the specific numerical values used for the positions of the ammonite fossils, apparently each author estimated the values independently from Macellari's (1986) Figure 6. In calculating the values in Table 4, we applied Solow's and Springer's methods to the values used throughout the rest of this paper in order to maintain comparability.)

Discussion and Conclusion

The method described in this paper extends the approach of Marshall (1995) for calculating confidence intervals for the position of a mass extinction boundary. Our method yields substantially narrower intervals, allowing us to estimate the position of an extinction boundary more precisely, an important task in correlating hypothesized mass extinctions with records of geologic events.

Care must be exercised in constructing the collection of taxa to be included in the confidence interval calculation. If taxa that go extinct before the hypothesized extinction boundary are erroneously added, an unrealistically high confidence level will result. For instance, in the scenario depicted in Figure 7, suppose we had included four additional taxa that (unbeknownst to us) had gone extinct before the other taxa. If the tops of their range extensions lie below the highest range extension of the other ten taxa, then the calculated confidence level of the interval in the figure would increase from 65% to $1 - (0.9)^{14} = 0.77$ or 77%. However, this apparent improvement would be an artifact caused by the presence of

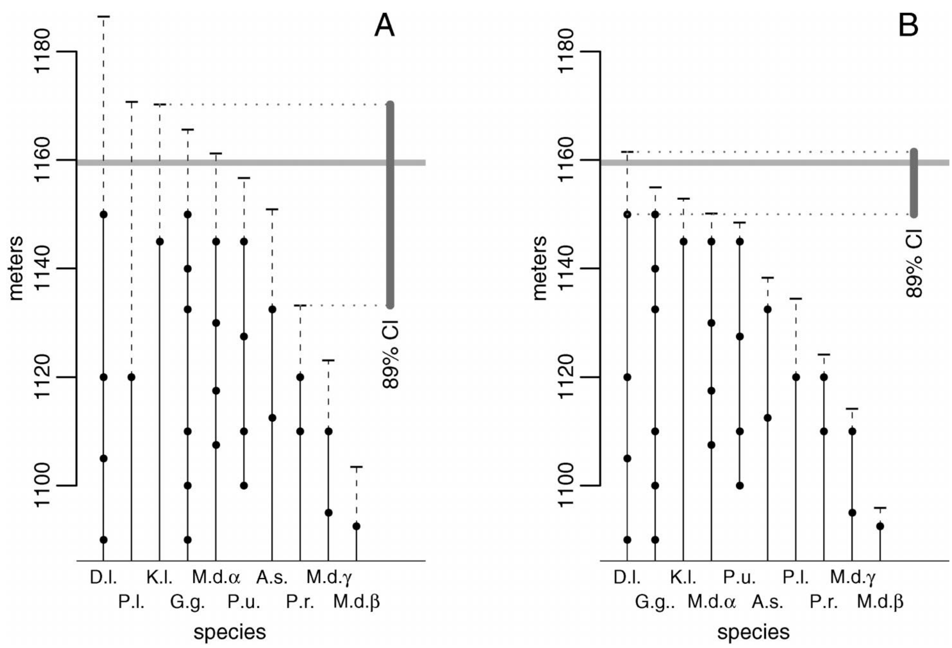

FIGURE 8. Range chart of ten ammonite species from the late Cretaceous of Seymour Island, Antarctica, collected by Macellari (1986). Species are as follows: *D. l.* = *Diplomocerus lambi*; *P. l.* = *Pseudophyllites loryi*; *K. l.* = *Kitchinites laurae*; *G. g.* = *Grossouvrites gemmatus*; *M. d.* α = *Maorites densicostatus* morphotype α; *P. u.* = *Pachydiscus ultimus; A. s.* = *Anagaudryceras seymouriense*; *P. r.* = *Pachydiscus riccardi*; *M. d.* γ = *Maorites densicostatus* morphotype γ; *M. d.* β = *Maorites densicostatus* morphotype β. Note that the taxa are ordered differently in the two panels. Horizontal gray line denotes position of iridium anomaly reported by Elliot et al. (1994). A, Vertical bar at right represents 89% confidence interval on the position of the mass extinction boundary, calculated by using 50% range extensions and the original Marshall (1995) calculation method. B, Vertical bar at right represents 89% confidence interval on the position of the mass extinction boundary, calculated by using 20% range extensions and the new calculation method. The confidence interval in Figure 8B is substantially narrower than that in Figure 8A, thus estimating the position of the extinction boundary more precisely.

TABLE 4. Confidence intervals on the position of the mass extinction boundary (assuming a simultaneous extinction occurred) for Seymour Island ammonite data (Macellari 1986) calculated with various methods. Units are meters above highest ammonite found. Because of the discreteness in the number of range extensions used in methods A–D, the confidence levels could be matched only approximately.

Method	Confidence level	Confidence interval	Width of interval
A. 50% range extensions, original Marshall (1995) calculation method	66%	(0.9, 15.6)	14.7
	89%	(−16.8, 20.2)	37.0
B. 20% range extensions, original Marshall (1995) calculation method	77%	(0.1, 11.5)	11.4
	86%	(−1.5, 11.5)	13.0
C. 50% range extensions, new calculation method	83%	(0, 15.6)	15.6
	95%	(0, 20.2)	20.2
D. 20% range extensions, new calculation method	62%	(0, 5.0)	5.0
	89%	(0, 11.5)	11.5
E. Maximum likelihood, Solow (1996)	62%	(0, 6.3)	6.3
	89%	(0, 15.7)	15.7
F. Uniformity of range extensions, Springer (1990)	62%	(0, 11.7)	11.7
	89%	(0, 17.5)	17.5

the four erroneously included taxa. To avoid such artificial inflation of the confidence level, it is essential to include only taxa that in fact went extinct at the hypothesized extinction boundary. Thus, before applying this (or any) confidence interval estimate, it is important first to test the assumption of simultaneous extinction of the taxa included. This may be accomplished by using existing tests (Springer 1990; Marshall 1995; Solow 1996); alternatively, a test may be carried out without selecting taxa (Solow and Smith 2000).

As is true of all methods, our method has limitations, and one can devise situations in which the method does not give a satisfactory answer. For example, if the tops of the range extensions for all taxa happen to be located at exactly the same height, the method will not be able to bound a confidence interval, and the interval will instead be a single point. Such a situation could arise, for instance, if all taxa have the same number of fossil horizons at exactly the same locations. In such a case, furthermore, the location of the highest find for each taxon will also be the same. We should then expect that the confidence interval for the position of the mass extinction boundary should be tight around this common location. Our method may place the confidence interval considerably higher, however, depending on the size of the range extensions. Admittedly, such a situation would be unlikely, and it would likely indicate a violation of the assumptions of independent and continuous sampling.

Unlike Solow's (1996) likelihood-based method, a strength of our method is that we need not assume uniform location of fossil horizons. Instead, by incorporating a generalized method such as Marshall's (1997) method of calculating range extensions for individual taxa, we may work with arbitrary preservation and recovery functions, making our method potentially applicable in a wide variety of situations.

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