Fossil Preservation and the Stratigraphic Ranges of Taxa

Mike Foote; David M. Raup

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Abstract.· ·The incompleteness of the fossil record hinders the inference of evolutionary rates and patterns. Here, we derive relationships among true taxonomic durations, preservation probability, and observed taxonomic ranges. We use these relationships to estimate original distributions of taxonomic durations, preservation probability, and completeness (proportion of taxa preserved), given only the observed ranges. No data on occurrences within the ranges of taxa are required. When preservation is random and the original distribution of durations is exponential, the inference of durations, preservability, and completeness is exact. However, reasonable approximations are possible given non-exponential duration distributions and temporal and taxonomic variation in preservability. Thus, the approaches we describe have great potential in studies of taphonomy, evolutionary rates and patterns, and genealogy.

Analyses of Upper Cambrian–Lower Ordovician trilobite species, Paleozoic crinoid genera, Jurassic bivalve species, and Cenozoic mammal species yield the following results: (1) The preservation probability inferred from stratigraphic ranges alone agrees with that inferred from the analysis of stratigraphic gaps when data on the latter are available. (2) Whereas median durations based on simple tabulations of observed ranges are biased by stratigraphic resolution, our estimates of median duration, extinction rate, and completeness are not biased. (3) The shorter geologic ranges of mammalian species relative to those of bivalves cannot be attributed to a difference in preservation potential. However, we cannot rule out the contribution of taxonomic practice to this difference. (4) In the groups studied, completeness (proportion of species [trilobites, bivalves, mammals] or genera [crinoids] preserved) ranges from 60% to 90%. The higher estimates of completeness at smaller geographic scales support previous suggestions that the incompleteness of the fossil record reflects loss of fossiliferous rock more than failure of species to enter the fossil record in the first place.

Mike Foote and David M. Raup. Department of the Geophysical Sciences, University of Chicago, Chicago, Illinois 60637

Incomplete Preservation and Stratigraphic Ranges

Nearly all aspects of evolutionary paleobiology are affected by the incompleteness of the fossil record. Because taxonomic durations potentially convey rich information on evolutionary rates (Simpson 1953; Van Valen 1973; Raup 1975, 1978; Stanley 1979), speciation patterns (Eldredge and Gould 1972; Cheetham 1986; Jackson and Cheetham 1994), and extinction mechanisms (Van Valen 1973, 1985a; Raup 1991; Marshall 1994a), it is crucial that we understand how observed (truncated) taxonomic ranges reflect true (original) durations (Shaw 1964; Paul 1982; Strauss and Sadler 1989; Marshall 1990, 1994b). The proportion of taxa that have left some fossil record (which we will refer to as *completeness*; cf. Valentine 1989) greatly influences our ability to understand evolutionary radiations (Valentine 1986; Wagner 1995), and to reconstruct genealogical

relationships (Fortey and Jefferies 1982; Fisher 1994; Smith 1994; Huelsenbeck 1994). Clearly, the probability of preservation per unit time, the proportion of taxa that are preserved, the distribution of original taxonomic durations, and the distribution of fossil ranges are all intimately related. Here, we develop an analytic approach that enables us to infer original duration distributions, preservation probability, and the proportion of taxa preserved, given only the readily available data on stratigraphic ranges, and without need of detailed information on occurrences within ranges. As illustrated with several empirical examples, this approach can uncover fundamental paleobiological information even in the face of an incomplete fossil record.

Consider the relationship between the original duration and the fossil range of a taxon (Fig. 1). Even when reported at a fine level of resolution, stratigraphic data are generally discrete by nature, and so we develop our ap-

True duration   Fossil range

15 m.y.   7 m.y.

15 m.y.   7 m.y.

10 m.y.   1 m.y.

$R = \text{Prob(preservation at least once in interval)}$
$(1 - R) = \text{Prob(non-preservation)}$

In general, Prob(range = t if duration = T):

$$= (1 - R)^T \qquad\qquad \text{if } t = 0$$
$$= T(1 - R)^{(T - 1)}R \qquad \text{if } t = 1$$
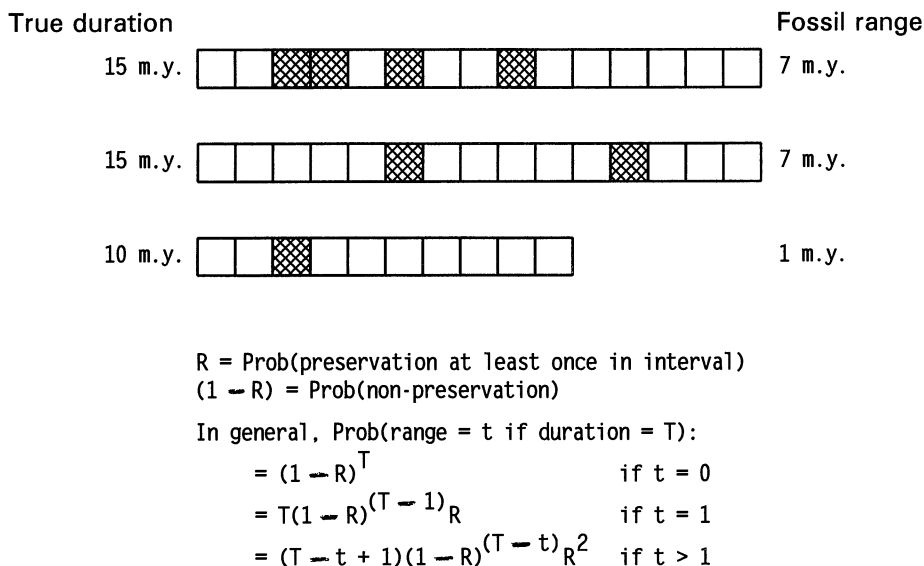$$= (T - t + 1)(1 - R)^{(T - t)}R^2 \quad \text{if } t > 1$$

FIGURE 1.   Relationship between taxonomic duration and fossil range. Time is in discrete intervals (here, one million years), and durations and ranges are treated as ranging through each interval of occurrence. Empty intervals indicate non-preservation; hatched intervals indicate preservation of taxon at least once during interval. Probability that taxon with true duration T has range t is easily derived (Appendix 1).

proach using discrete time intervals. Note that by *single occurrence* or *single hit* we mean preservation in only one interval of time; the taxon can in fact be widespread and abundantly preserved during this interval, or it can be confined to a single bedding plane or even a single specimen. The *range* of a taxon we take to be the number of intervals from its first to last occurrence, inclusive. Thus, single hits have a range of one interval (rather than zero), taxa confined to two adjacent intervals have a range of two intervals, and so on. While this may differ from commonly applied conventions (e.g., Dodson 1990), we emphasize that, in the context of what we develop below, treating single hits as having unit range is not an approximation. Rather, it is a crucial aspect of our quantitative approach, on which depend several important results.

If we assume that preservation is random in time and among taxa with some constant average probability, R (an assumption we relax below), then it is straightforward to determine the probability that a taxon with a given true duration will have a given observed range (Fig. 1, Appendix 1). Therefore, we can analytically degrade an entire distribution of original durations into an expected distribu-

tion of observed fossil ranges. To illustrate this, we consider an initially exponential distribution of durations, corresponding to constant extinction probability, q (Van Valen 1973). Figure 2 illustrates the degradation of taxonomic ranges for the case where $q=0.1$ and $R=0.2$. Note that in this and all subsequent figures, we plot raw rather than cumulative frequencies, thus avoiding the forced regularity that often comes with cumulative survivorship curves (Raup 1975).

Because long-lived taxa are more likely to be preserved than short-lived taxa, the original durations of preserved taxa are biased upward (Fig. 2B). This bias is greater as preservation probability decreases. The fossil ranges are dominated by single hits (see also Buzas et al. 1982), and the median range is substantially less than the true median duration (Fig. 2C). As preservation probability decreases, the frequency of single hits increases and the median range decreases.

On a semi-log plot, the initial survivorship curve is linear with a slope whose absolute value is equal to the extinction rate (Fig. 2A). In preparing graphs such as Figure 2, we discovered, quite by accident, a most remarkable result (Fig. 2C). *If we ignore single hits, the re-*
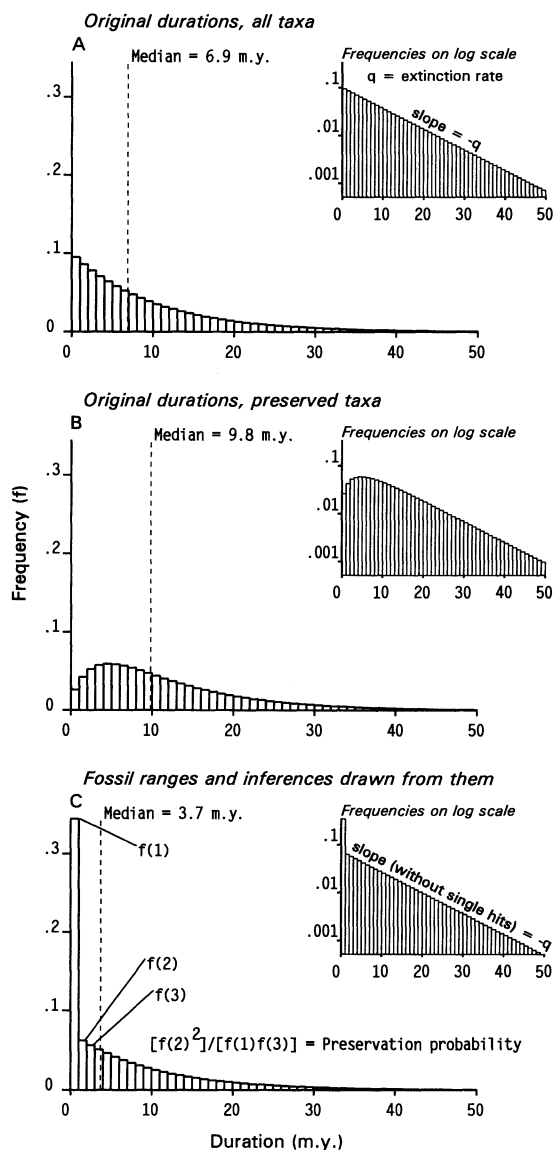
Original durations, all taxa

Original durations, preserved taxa

Fossil ranges and inferences drawn from them

Duration (m.y.)

FIGURE 2. Analytic degradation of initially exponential distribution of taxonomic durations, corresponding to extinction rate (q) of 0.1 per taxon per million years, and preservation probability (R) of 0.2 per taxon per million years. Frequencies in this and all subsequent figures are raw values, not cumulative frequencies. A, Original durations. Duration-frequency relationship is linear on a semi-log plot, and this relationship has slope equal to $-q$. B, Original durations of the subset of taxa preserved at least once (in this case, 72% of taxa). Because shorter-lived taxa are less likely to be preserved, fossil taxa represent a biased subset having longer durations on average. C, Fossil ranges of preserved taxa. Because of truncation, the median range is shorter than the true median duration. *If single hits are ignored*, the remaining range-frequency relationship is log-linear with slope equal to $-q$ (Appendix 2). Thus, fossil ranges can be used to estimate the true extinction rate. The range-frequency ratio (FreqRat), i.e., $[f(2)^2]/[f(1)f(3)]$ is exactly equal to the probability of preservation, R (Appendix 3). Thus, fossil ranges can be used to estimate preservation potential and completeness.

mainder of the range-frequency distribution is also log-linear with the same slope as the distribution of original durations. Thus, if the original durations are exponentially distributed, we can recover the true extinction rate (thus the true median duration) given only the preserved fossil ranges. (A derivation of this result, developed after the fact, is given in Appendix 2.)

Another accidental discovery, equally remarkable, is that the preservation probability is only barely concealed within the range-frequency distribution. *If we denote the frequency of taxa with observed ranges of one, two, and three intervals, respectively, as f(1), f(2), and f(3), then the preservation probability R is exactly equal to $f(2)^2/[f(1)f(3)]$.* We will hereafter refer to this range-frequency ratio as the *FreqRat*. Thus, given only the observed range-frequency distribution, one can estimate the preservation probability. Along with the recovered distribution of original durations, this easily leads to an estimate of the proportion of taxa preserved (Appendix 1). Again, only observed ranges are required; no information on occurrences within taxonomic ranges is needed. (See Appendix 3 for a derivation of this result.)

Of course, the results that preserved ranges are shorter than true durations and that preserved taxa generally represent a biased sample of the original durations, are true not only of originally exponential distributions of durations. To our surprise, we have found that *the FreqRat gives a very good estimate of preservation probability even for initial duration distributions that are not exponential* (see Appendix 4 for derivation). For example, for the contrived distribution illustrated in Figure 3, the true preservation probability is equal to 0.15, while the FreqRat is equal to 0.1504. This close correspondence between true and estimated preservation probability also holds for other values of R. Taking the distribution in Figure 3A and varying R from 0.01 to 0.99, the greatest difference between true and estimated preservation probability is less than 1 percent. In fact, we have found that the FreqRat provides a good estimate of preservation probability for such a diversity of duration distributions that we must go to great lengths to make it fail. If the taxonomic duration frequencies are uni-
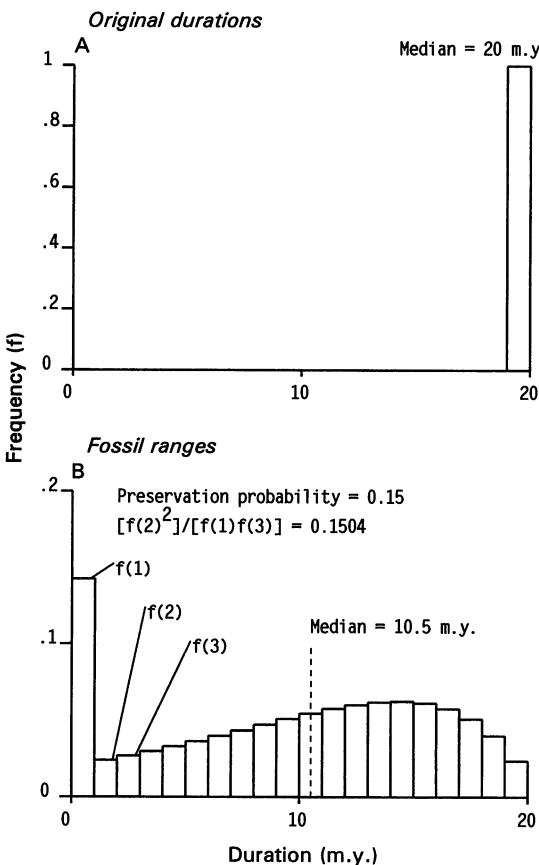
Original durations

Fossil ranges

FIGURE 3. Analytic degradation of duration distribution in which all taxa have the same duration, and in which preservation probability is equal to 0.15 per taxon per million years. The FreqRat (0.1504) in this case is approximately equal to the preservation probability (Appendix 4). 96% of taxa are preserved at least once.

TABLE 1. FreqRat for 100 distributions of taxonomic durations in which frequencies are drawn randomly from uniform distribution.

True preservation probability per interval (R)	Mean	FreqRat		Standard deviation
		Minimum	Maximum	
0.01	0.0101	0.00998	0.0102	0.000038
0.05	0.0503	0.0496	0.0509	0.00027
0.1	0.100	0.0974	0.103	0.0011
0.2	0.201	0.189	0.222	0.0061
0.3	0.301	0.253	0.354	0.019
0.4	0.411	0.296	0.533	0.049
0.5	0.525	0.289	0.889	0.12
0.6	0.655	0.230	1.44	0.24
0.7	0.805	0.241	3.75	0.48
0.8	0.99	0.0731	4.74	0.83
0.9	1.63	0.0404	14.0	2.3

yield predicted range distributions that agree well with the one observed. Such a procedure is illustrated in Figure 4. Here, an initially exponential distribution of durations (extinction rate equal to 0.25 per lineage per time unit) is degraded with a preservation probability of 0.5 per lineage per time unit to yield the observed ranges in the upper right panel.

Our goal is to recover the initial duration distribution, given only the observed ranges, and without assuming the form of the distribution. We first estimate R using the FreqRat. Then, an initial distribution of durations is arbitrarily chosen, here a uniform distribution, and the predicted distribution of ranges is compared to that observed. The deviation between predicted and observed distributions is computed as

$$D = \Sigma |\log(\text{predicted frequency}) - \log(\text{observed frequency})|$$

The initial distribution is then perturbed slightly, by adding small random numbers (with mean zero) to the frequencies, and the deviation is recalculated. If the new deviation is less than the previous deviation, the perturbed distribution is accepted as a better candidate. At each iteration of this procedure, the candidate distribution of durations is perturbed repeatedly until a better fit between predicted and observed ranges is obtained. The fit is accepted when the deviation between predicted and observed ranges is tolerably low, or when many further perturbations no longer improve the fit. In the case at

formly distributed random numbers, a situation we consider highly unnatural, then the FreqRat works well for low to moderate preservation probabilities, but performs poorly at higher preservation probabilities (Table 1).

The FreqRat allows an estimate of preservation probability (R), but the distribution of fossil ranges alone yields the original duration distribution only if the latter is exponential. However, a given original distribution (which we seek), filtered through a given preservation probability (for which we have an estimate), predicts a unique distribution of fossil ranges (which we observe directly). Therefore, we should be able, by brute force, to explore various candidates for original duration distributions in order to determine which of them
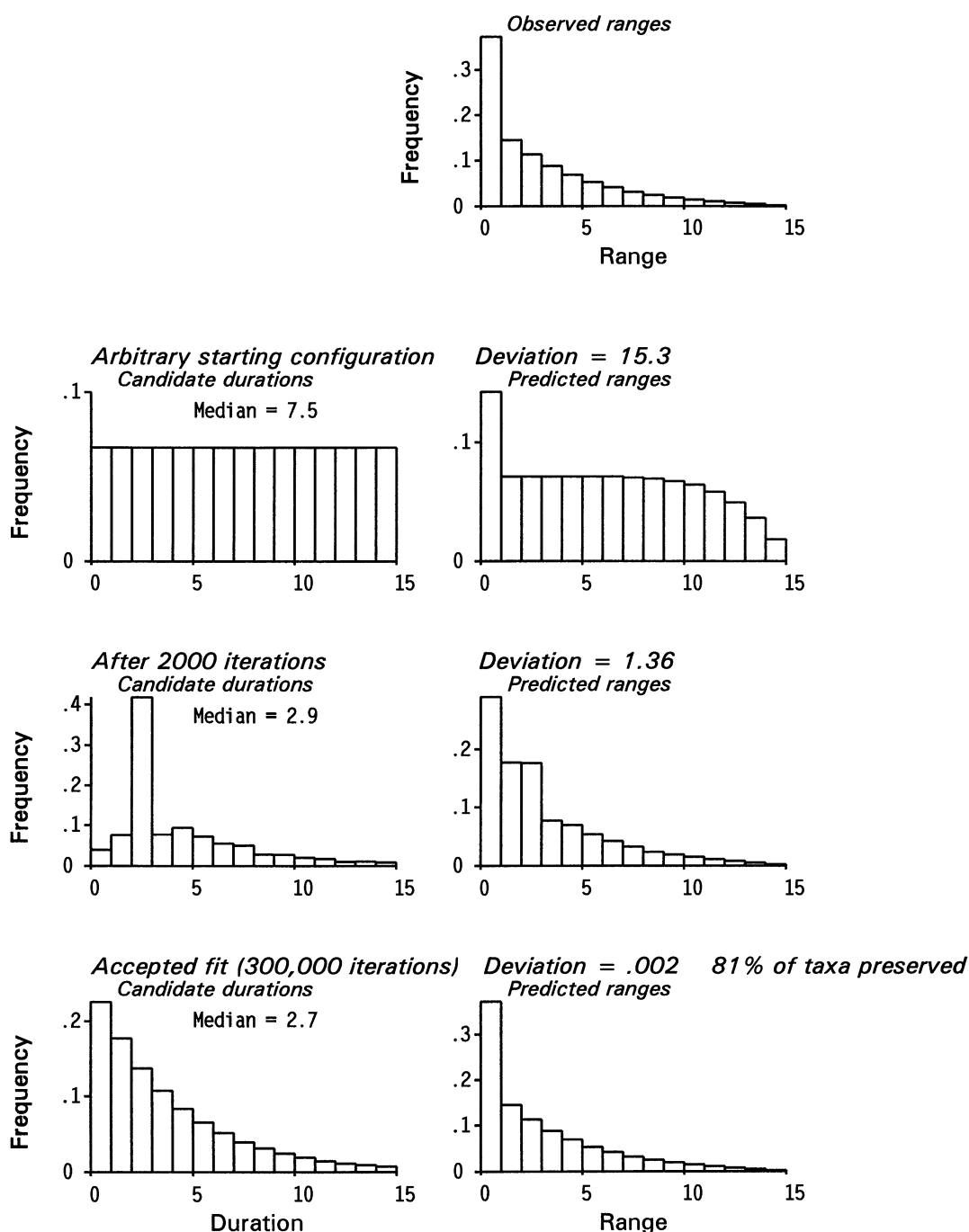
FIGURE 4. Illustration of trial-and-error method for fitting an original duration distribution to an observed distribution of fossil ranges. The preservation probability is estimated using the FreqRat for the observed ranges (upper right panel). The method starts with an arbitrary distribution of original durations (left panel). The estimated preservation probability yields a predicted distribution of ranges (right panel), which is then compared to the observed ranges (upper right panel). The original duration frequencies are then perturbed randomly in small increments until the predicted ranges are in better agreement with the observed ranges. This original duration distribution then becomes the best candidate. This process is repeated until a tolerable deviation between expected and observed ranges is obtained, or until many further iterations result in no improvement in the fit. In the example here, the observed ranges are based on the degradation of an initially exponential distribution of durations, with extinction rate 0.25 and preservation probability 0.5. After 300,000 iterations, the procedure accurately reconstructs the original exponential distribution.
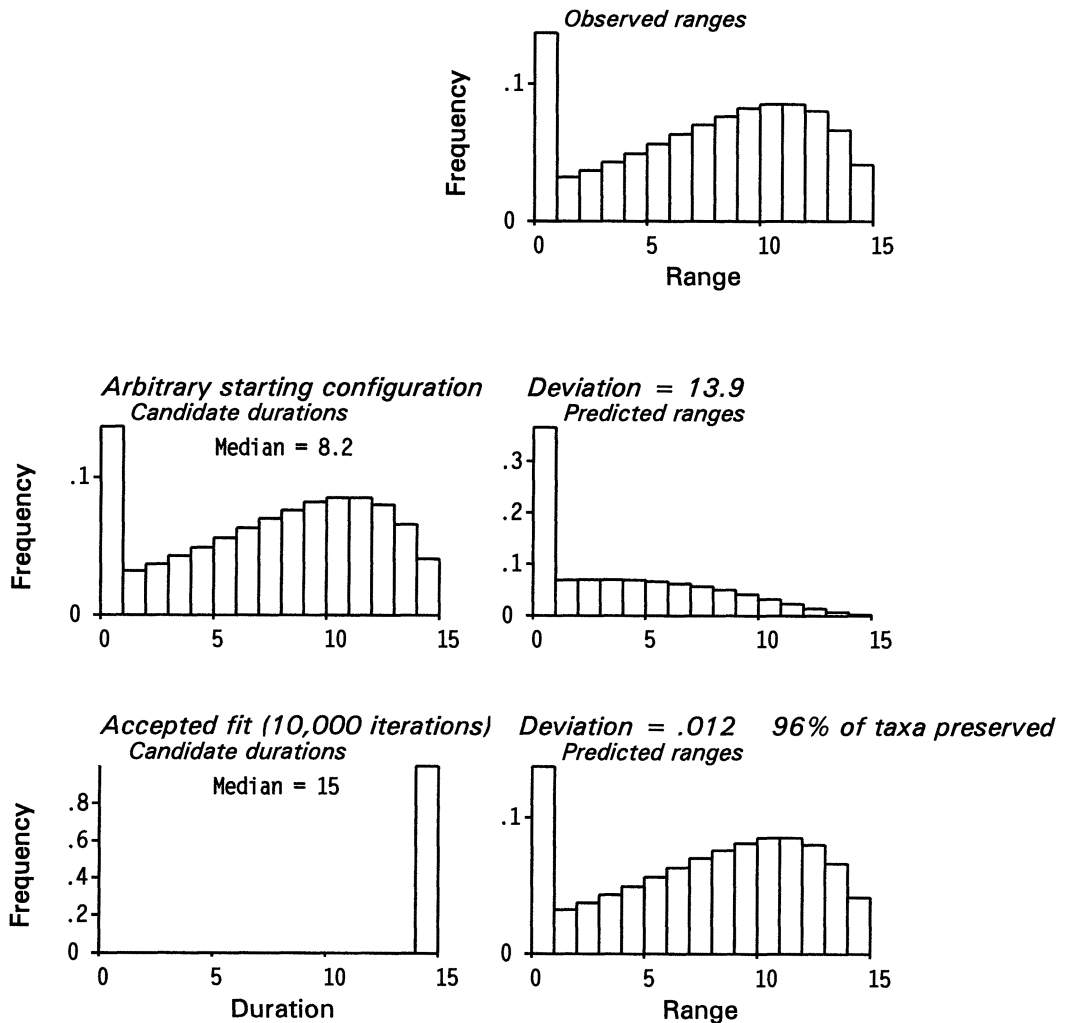
FIGURE 5. Further illustration of trial-and-error method for fitting an original distribution to an observed distribution of fossil ranges. In this case, a single duration category (15 m.y.) was degraded with a preservation probability of 0.2 per million years. After 10,000 iterations, the initial distribution of durations is accurately reconstructed.

hand, this procedure is able to recover the initial exponential distribution of durations, which we know to be correct. In another test of this approach, we can recover an initial distribution in which all taxa have a duration of 15 million years (Fig. 5).

How quickly a stable solution is obtained depends on the arbitrary starting configuration, the true initial distribution, the preservation probability, the magnitude of perturbations, and the method of optimization (e.g., straight hill climbing versus simulated annealing; Press et al. 1986). Therefore, we are unable to generalize about computational efficiency. We do not know that a unique solution can be obtained by this procedure, but our success in recovering a number of other known distributions, using different starting configurations, preservation probabilities, perturbation magnitudes, and optimization methods, suggests that the approach has great potential. We will apply this approach below in a case where we suspect that the assumption of log-linear survivorship may be strongly violated.

Clearly, it is not preservation probability alone that dictates the quality of the fossil record, but preservation probability with respect to the distribution of true durations. With lower extinction rates, i.e., longer durations, taxa are more likely to be preserved at least once,
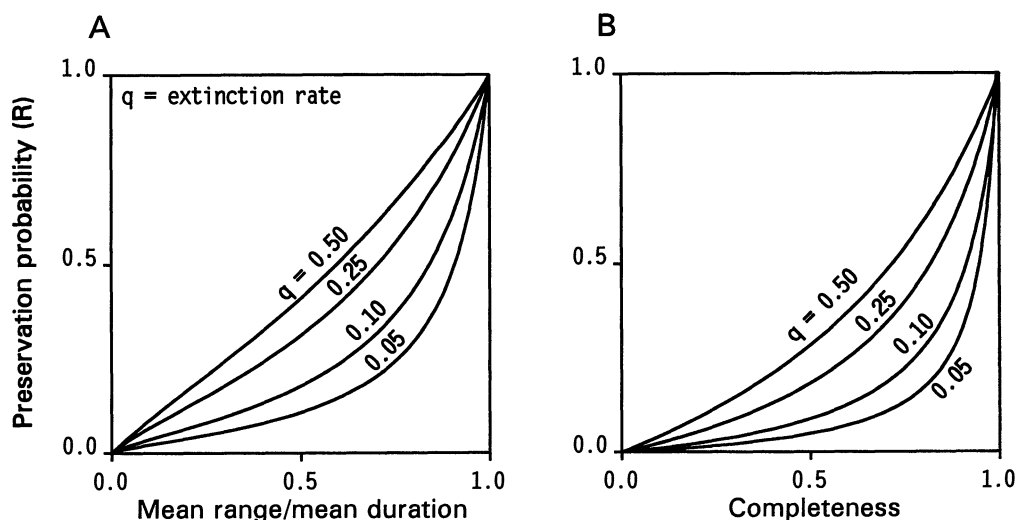
FIGURE 6. Relationship between preservation probability per unit time (R) and (A) mean range, including taxa confined to a single interval, divided by true mean duration, and (B) completeness (i.e., proportion of taxa preserved at least once), for the case of time-homogeneous extinction (i.e., exponential distribution of durations). In each panel, the four curves from upper left to lower right correspond to extinction rates of 0.5, 0.25, 0.1, and 0.05 extinctions per taxon per million years, respectively. Corresponding mean durations are 2 m.y., 4 m.y., 10 m.y., and 20 m.y. For a given probability of preservation, the fossil record is more complete if extinction rate is lower. With shorter durations, the fidelity of the fossil record (in terms of completeness and the ability of mean ranges to reflect true durations) improves substantially as preservation probability increases. However, with lower extinction rates, the fossil record is rather faithful even at low probabilities of preservation, and further increases in preservation probability yield diminishing returns.

and a lower time-specific preservation probability is therefore required to yield a given level of completeness. Figure 6 illustrates the effect of preservation probability on the relationship between mean duration and mean range, and on completeness, for several values of extinction rate. With very high extinction rates, increases in preservation probability yield nearly proportional increases in the quality of the fossil record. At lower extinction rates, there is something of a "saturation effect." The fossil record is rather faithful even at low preservation probabilities, so that further enhancement of preservation potential has a small effect on the overall quality of the record (as measured by completeness or by the ability of mean range, taken at face value, to reflect mean original duration).

To summarize, assuming stochastically constant preservation probability, the distribution of ranges allows one to estimate the probability of preservation per taxon per interval of time (R). Further assuming an exponential distribution of original durations (i.e., constant extinction rate), one can recover the ini-

tial distribution from the ranges alone, because the range frequencies beyond the single hits are log-linear with the same slope as that of the original durations. If log-linear survivorship cannot be assumed, then an estimate of the original durations can be obtained by a brute-force fitting procedure. The estimate of preservation probability, combined with the estimate for the original durations, yields an estimate of the proportion of taxa that are preserved in the fossil record.

Tests and Applications

Upper Cambrian–Lower Ordovician trilobite species.—Stitt (1977) has documented the occurrences of over 100 trilobite species in a single measured section from the Upper Cambrian and Lower Ordovician of Oklahoma. His data allow a test of our method (Table 2, Fig. 7A). Although there is artificial range truncation at the top and bottom of the section, this affects a small proportion of taxa and is negligible if, as in this case, the section is thick relative to the average stratigraphic range of taxa. The maximum interval through

TABLE 2. Estimated median duration, preservation probability, and completeness for data analyzed here. Standard deviations are based on simulation procedure described in text.

Data (number of taxa)	Sources	Median duration (m.y.)	S.D.	Preservation probability	S.D.	Com-plete-ness	S.D.
Upper Cambrian–Lower Ordo-vician trilobite species from Oklahoma (101)	Stitt 1977	0.15	0.05	0.73 per 60-foot interval	0.25	0.9	0.029
Ordovician–Devonian crinoid genera (global) (395)	Bassler and Moodey 1943; Webster 1969–1993; Foote 1994a	7	1.8	0.5 per strati-graphic inter-val (mainly series and stages)	0.082	0.7	0.018
Cenozoic mammal species from North America (2941)	J. Alroy pers. comm. 1995; after Alroy 1994	1.7	0.1	0.25 per 0.7-m.y. interval	0.016	0.6	0.007
European Jurassic bivalve spe-cies (321)	Hallam 1976	8.0	1.0	0.87 per 5-m.y. interval	0.16	0.9	0.012

which data were not collected in this section is 59 feet, call it 60 feet (18.3 m). This represents the finest resolution we can hope to have throughout the section. Therefore, we divided the section into 60-foot intervals, and for each species recorded the total range and the number of intervals in which it is actually preserved. (This approach to stratigraphic binning removes one of the causes of flat-topped survivorship curves; see Raup 1975; Sepkoski 1975.)

The FreqRat for these data is equal to 0.73, which serves as our estimate of preservation probability per species per 60-foot interval. This ratio predicts that, of all the intervals within the ranges of species (*excluding first and last intervals of preservation*; cf. Paul 1982), 27% should be empty and 73% should be filled. In fact, 31% are empty, a remarkably good agreement which is well within the range of bino-mial sampling error (n = 107 intervals; two-tailed p = 0.45). The dashed line in Figure 7A shows a least-squares linear regression based on the frequencies beyond the single hits. The data are in close agreement with the linear fit, suggesting that an exponential survivorship model may be appropriate. The frequency of single hits predicted by our method is also close to that observed. For these data we esti-mate a median duration of 2.0 60-foot inter-vals, which we estimate to be on the order of 150,000 years (calibration based on Stitt 1977; Ludvigsen and Westrop 1985; Harland et al. 1990; and Bowring et al. 1993; cf. Foote 1988).

Assuming an intially exponential distribu-tion of durations, we estimate completeness in this section as 90%. This estimate may seem high at first. Surely, even the most optimistic paleontologists would not think that 90% of all well-skeletonized species that have ever lived are preserved. However, this estimate is for local completeness in this section, not glob-al completeness. In fact, it does not differ sub-stantially from the figures given by Schopf (1978) and Valentine (1989) for the proportion of well-skeletonized genera and species likely to enter the fossil record (regardless of wheth-er they are subsequently lost). Our result is thus quite in line with Valentine's suggestion that incompleteness in well-preserved groups largely reflects the loss of fossiliferous rock rather than failure of species to enter the fossil record.

Paleozoic crinoid genera.—The preservation probability of a supraspecific taxon should, in principle, vary over time as the number of con-stituent species varies. However, as a first ap-proximation, we will treat the preservation probability as constant. Below, we explore the effect of systematic variation in preservation probability and suggest that our approach is robust to such variation. Appendices 5 and 6 derive the relationship between original du-rations and observed ranges of genera when speciation rate, species-level extinction rate, and species-level preservation probability are stochastically constant.

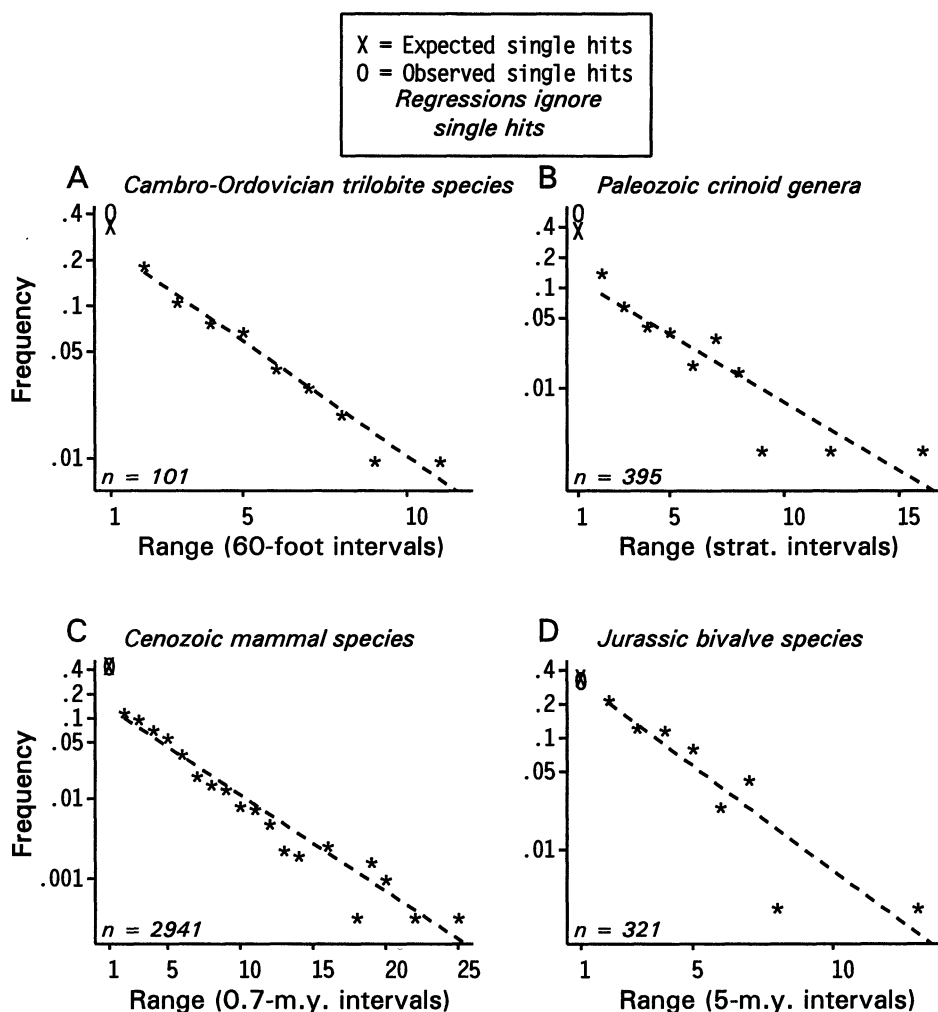Stratigraphic ranges of crinoid genera were

FIGURE 7. Analysis of stratigraphic ranges of fossil taxa. Plot of range-frequency distribution is semi-logarithmic, and dashed line is least squares linear regression through points representing ranges of two or more intervals. A, Upper Cambrian and Lower Ordovician trilobite species from Oklahoma (data from Stitt 1977). Estimated median duration is 2.0 intervals (ca. 150,000 yr.). Estimated preservation probability based on FreqRat is 0.73. Corresponding completeness estimate is 90%. B, Crinoid genera originating before the Carboniferous (data based on Bassler and Moodey 1943; Webster 1969, 1977, 1986, 1988, 1993; Foote 1994a). Estimated preservation probability is 0.5 per genus per interval (see text for description of intervals). Number of taxa confined to a single interval is greater than expected under model of exponential duration distribution and random preservation. C, Cenozoic mammal species of North America (data from Alroy, pers. comm. 1995, after Alroy 1994). Estimated extinction rate is 0.28 per 0.7-m.y. interval, implying a median duration of 1.7 m.y. Estimated preservation probability is 0.25 per 0.7-m.y. interval, with a corresponding completeness of 58%. D, European Jurassic bivalve species (data from Hallam 1976). Estimated extinction rate is 0.43 per 5-m.y. interval, implying a median duration of 8.0 m.y. Estimated preservation probability is 0.87 per 5-m.y. interval, with a corresponding completeness of 90%. Although the bivalve record is more complete than that of mammals, the great difference in our estimates of true median duration for the two groups suggests that the shorter stratigraphic ranges of mammals are not solely artifacts of preservation.

taken from the compilation of Foote (1994a), based mainly on the bibliographies of Bassler and Moodey (1943) and Webster (1969, 1977, 1986, 1988, 1993). Because there seem to be greater taxonomic problems in the Carbonif-

erous and Permian, only genera originating before the Carboniferous were considered. In order to test our method, we used the same bibliographic sources to determine occurrences of genera within the observed range.

The stratigraphic intervals used were mainly conventional series and stages, with an average duration of about 7 m.y. All told, there were 395 genera whose occurrences could be placed in these intervals.

Using the FreqRat, and ignoring the variation in the duration of stratigraphic intervals (see discussion under *European Jurassic bivalve species*, below), we estimate the preservation probability per genus per interval as 0.5 (Table 2, Fig. 7B). This allows us to predict that 50% of the intervals within the range of a genus (excluding endpoints) should not actually contain preserved species belonging to that genus. Of a total of 266 internal intervals, 121 (45.5%) represent gaps while 145 are filled. This is quite close to the prediction of our estimated preservation probability, and is well within binomial sampling error (two-tailed p = 0.16).

If we accepted the assumption of an originally exponential distribution of durations, we would estimate the extinction rate as 0.31 per genus per interval, with a corresponding median duration of 2.2 intervals, or 15.4 m.y. The corresponding proportion of genera preserved would be 0.8. However, agreement with the exponential model is poorer than for trilobite species. In particular, the number of taxa confined to a single interval or to two adjacent intervals is more than expected under the model. On the basis of simulations such as that presented below (Variability in Estimates of Extinction Rate and Completeness), we find that the number of single hits is significantly greater than expected under a model of constant extinction rate ($p < 0.001$). This makes sense, since genera are expected to show concave survivorship curves on semi-log plots even if their constituent species show log-linear survivorship (Raup 1978, 1985).

Given the deviation from the exponential model, we prefer our brute-force approach to fitting an initial distribution of durations (Fig. 8). We thus estimate that the median duration was 1 interval, or 7 m.y., and that completeness is on the order of 0.7. Note that our inability to obtain as clean a fit as in the foregoing idealized cases (Figs. 4 and 5) partly reflects the fact that deviations are measured logarithmically. Thus, when the expected fre-

quency is low, a small number of taxa can have a large effect on the calculated deviation. The quality of fit is also affected by unequal interval lengths and temporal variation in preservation probability.

Because the crinoid data are global in scale, one might have expected a lower estimate of completeness than that obtained (cf. trilobite data above). However, the expected tendency for global completeness to be lower than completeness in local, well-preserved sections seems to be offset somewhat by the use of genera, which endure longer (see Fig. 6) and may have several contemporaneous species. The relatively high preservation probability of crinoid genera suggests that our preferred approach should yield an estimate of median duration similar to an approach that takes ranges at face value as representative of durations (e.g., Baumiller 1993). In fact, our estimate of median genus duration is somewhat higher than those of Baumiller (1993: Table 1), although our restriction to pre-Carboniferous genera hinders the comparison.

Cenozoic mammal species.—As part of a comprehensive revision of the mammalian biochronology of North America, Alroy (1992, 1994) has estimated the stratigraphic ranges of over three thousand species of Cretaceous and Cenozoic mammals, which he has kindly provided to us. Ranges are best constrained for taxa confined to the Cenozoic (J. Alroy personal communication 1995), and so we have confined our analysis to these taxa. To reduce problems with living taxa (Raup 1975, 1991; Van Valen 1979), we have also confined our analysis to extinct species. These culling procedures leave a total of 2941 species. We have adopted Alroy's suggestion (1996; personal communication 1995) to use 0.7-m.y. intervals, but we explore the effect of stratigraphic resolution below. These data fit the exponential survivorship model rather well, and the predicted frequency of single hits is in close agreement with the observed frequency (Fig. 7C). The FreqRat yields an estimated preservation probability of 0.25 per interval. Using the assumption of an initially exponential distribution of durations, we estimate the extinction rate as 0.28 per interval, with a corre-
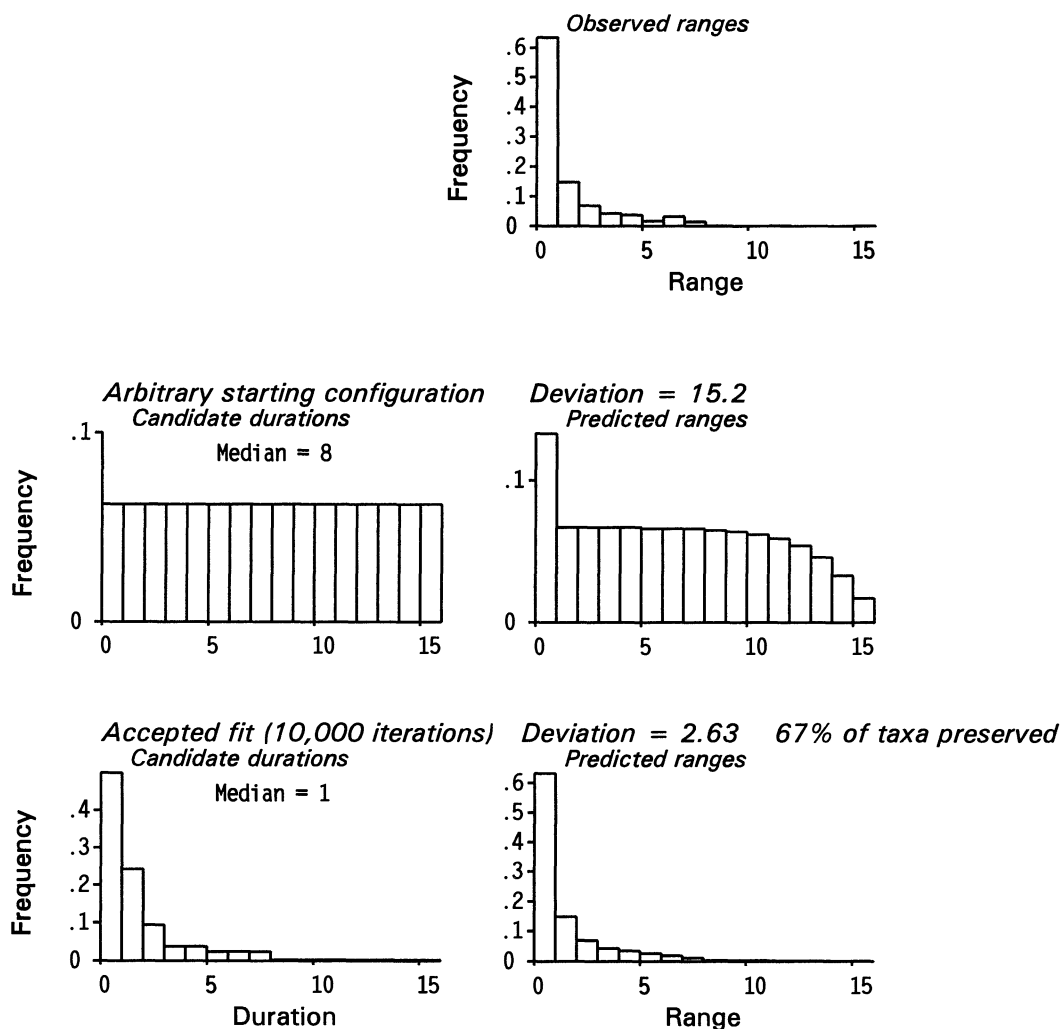
FIGURE 8. Application of trial-and-error method to estimating original distributions of crinoid genera. This method is applied because of deviation from exponential model (Fig. 7B). Because we generally expect many short-lived and fewer long-lived genera (Raup 1978, 1985), the fitting procedure was modified to allow only monotonic distributions of original durations. The results are similar when this constraint is not applied. The estimated distribution of durations implies a median duration of 1 interval (about 7.0 m.y.), and a corresponding completeness of 67%.

sponding median duration of 1.7 m.y. and a corresponding completeness of 58% (Table 2).

European Jurassic bivalve species.—A classic comparison of taxonomic rates is that between mammals and bivalves (e.g., Simpson 1953; Stanley 1979; Van Valen 1985b). However, if mammals have a lower preservation probability than bivalves, the shorter ranges of mammals could be a preservational artifact. To explore this possibility, we have analyzed the stratigraphic ranges of European Jurassic bivalve species as presented by Hallam (1976).

Hallam gives first and last occurrences to the stage and substage level. Given substantial variation in interval length, we have converted these occurrences to approximate ranges, using the time scale of Harland et al. (1990) and placing origins at (sub)stage midpoints and extinctions at (sub)stage endpoints (cf. Van Valen 1973; Sepkoski 1975) (Fig. 7D). Other conventions, such as placing origins at the bases of intervals, coarsening substage-level data up to the stage level, or assuming equal-length intervals, yield comparable results. We esti-
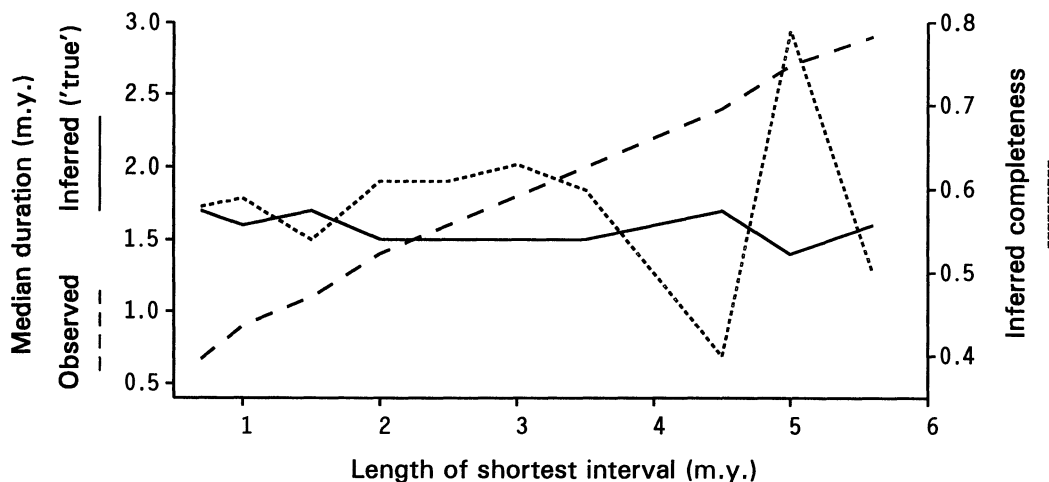
FIGURE 9.   Effect of stratigraphic resolution on analysis of fossil ranges, illustrated with data on mammal species. Dashed curve shows that estimates of median duration that take ranges at face value are biased, increasing as stratigraphic resolution becomes coarser. Solid curve shows that the true median duration, inferred using the method of this paper, is not biased. Likewise, dotted curve shows that our approach to estimating paleontologic completeness is not biased by stratigraphic resolution. However, estimates become highly variable when intervals are long relative to true median duration.

mate that completeness is higher for bivalves (90%) than for mammals (Table 2). However, our estimate of true median duration (8.0 m.y.) is nearly five times higher for bivalve species than for mammal species. Thus, we can say with some confidence that the apparent difference in taxonomic longevity between bivalves and mammals is not solely a preservational artifact.

We cannot rule out the possibility that these differences in duration and completeness may reflect taxonomic artifact (Simpson 1953). The probability that a species is preserved at least once has two components, the probability of preservation per unit time and the duration of the species (Fig. 6). Therefore, a broader species concept would inflate completeness as well as stratigraphic ranges. Nevertheless, it appears that the preservation probability per unit time is greater for bivalves than for mammals. The comparison is difficult as presented in Table 2, since the values of R were calculated at different scales of temporal resolution. However, using the same general approach outlined in Appendix 1, we can show that, given a median duration of 8.0 m.y., the preservation probability of bivalves would have to be about 0.37 per 0.7-m.y. interval (compared to 0.25 for mammals) in order to yield the es-

timated preservation probability of 0.87 per 5.0-m.y. interval.

Effects of Stratigraphic Resolution

Analyses of taxonomic data often reflect problems of stratigraphic binning. The size of the intervals into which data are lumped can affect estimates of average duration and extinction intensity, for example (Raup 1975; Sepkoski 1975; Foote 1994b). Our approach for estimating duration distributions and preservation potential should not, ideally, be biased by the coarseness of intervals (see Appendices). However, we would expect that, if stratigraphic intervals are very long relative to median duration, then nearly all taxa would be confined to one interval and the uncertainty in our approach, which relies on the number of taxa with ranges of two intervals, three intervals, and so on, would become intolerable.

The size and quality of Alroy's data set allow us to explore the effects of stratigraphic resolution (Fig. 9). As expected, the observed median range, taken at face value, increases steadily as stratigraphic resolution becomes coarser. Taxa confined to a single 5-m.y. interval may have a range of only 0.1 m.y., for example, but this cannot be discerned from the binned data. Note that the estimate of median

duration that takes the record at face value can either overestimate or underestimate the true duration. Range truncation dominates when stratigraphic resolution is fine, but it is progressively outweighed by the artificial extension of ranges caused by stratigraphic binning when intervals become coarser.

In contrast to observed ranges, our estimates of original durations are not systematically biased by stratigraphic resolution, at least not over the range of stratigraphic bin sizes explored here. Estimated completeness is also unbiased. However, for this data set, once the smallest stratigraphic interval is about twice the true median duration, estimates of completeness become very noisy. Note that, while completeness is not biased by interval length, the probability of preservation per interval (R) must, by its very nature, increase with interval length.

Variability in Estimates of Extinction Rate and Completeness

Like other analyses of survivorship, the approach presented here is a statistical method that is more reliable as more taxa are incorporated. We have performed simulations to explore the variance associated with estimated extinction rate and completeness, using the parameters derived from our empirical cases (Table 2). For example, for mammals the estimated completeness of 58% implies that the 2941 preserved species represent 5070 initial species. Therefore, 5070 durations were drawn randomly from an exponential distribution corresponding to an extinction rate of 0.28. The degradation of these ranges was simulated according to the estimated probability of preservation of 0.25 per interval. The extinction rate and preservation probability were estimated from the resulting distribution of ranges, and from these the completeness was calculated. Simulations were repeated 1000 times to estimate the variance in parameters to be expected from sampling error under the time-homogeneous preservation model. The results show that, for large data sets, the sampling error is negligible, and reliable estimates of extinction rate and completeness are obtained (Table 2). Of course, for smaller sample sizes, the variance increases. Comparable sim-

ulations were performed with different numbers of species (results not presented). As expected, the standard error increases roughly as $1/\sqrt{N}$, but most simulations still yield estimates fairly close to the mean. With moderate sample sizes and time-homogeneous preservation, our method provides a reliable way to estimate extinction rates and completeness.

Taxonomic Variation in Preservation Probability

Because of differences in structure and habitat, species within the same higher taxon vary in their preservation potential. The effect of this variation on our approach can be investigated analytically by applying the results of Appendix 1 to mixtures of taxa with different preservation probabilities. We have explored many cases, including equal mixtures of taxa as well as mixtures containing a predominance of either more poorly preserved or better preserved taxa (Table 3). Interestingly, we have found that the FreqRat does not yield the true average preservation probability, but it does accurately estimate the "effective" preservation probability. That is, if we treat the range-frequency distribution as if it represented the result of homogeneous preservation, then the FreqRat, combined with the extinction rate which is accurately estimated from the mixed data, yields an accurate estimate of the proportion of taxa preserved. Thus, we conclude that analysis of range-frequency distributions allows inference of true extinction rates and paleontologic completeness even if the assumption of constant preservation potential among taxa is violated. We emphasize that the FreqRat is a statistical property of a data set. If there is taxonomic variation in preservation probability, the average preservation probability should not be applied to the ranges of single taxa.

Temporal Variation in Preservation Probability

The quality of preservation on the outcrop scale varies along a spectrum from barren intervals to *Lagerstätten*. On larger geographic and temporal scales, relevant to most of the examples discussed here, this smaller-scale variation is averaged out to some extent. A

TABLE 3. Examples of effect of taxonomic variation in preservation probability on estimates of extinction rate, mean preservation probability, and completeness.

Model	Extinction rate		Mean preservation probability		Completeness	
	Actual	Estimated	Actual	Estimated	Actual	Estimated
Equal numbers of taxa with preservation probabilities equal to 0.1, 0.2, 0.3, 0.4, 0.5, 0.6, 0.7, and 0.8	0.25	0.25	0.45	0.37	0.73	0.73
Equal numbers of taxa with preservation probabilities equal to 0.01, 0.02, 0.03, 0.04, 0.05, 0.06, 0.07, and 0.08	0.25	0.25	0.045	0.043	0.17	0.17
50% of taxa with preservation probability equal to 0.1, 37.5% with preservation probability equal to 0.25, and 12.5% with preservation probability equal to 0.5	0.25	0.25	0.21	0.18	0.49	0.49
50% of taxa with preservation probability equal to 0.5, 37.5% with preservation probability equal to 0.25, and 12.5% with preservation probability equal to 0.1	0.25	0.25	0.36	0.32	0.68	0.68

million years with no fossils is uncommon, as is a million-year-long fossil bonanza. Nevertheless, there is temporal variability in preservation potential. To explore the effect of this variability, we have performed further simulations (not presented), using the preservation probability estimated for mammals as a mean value. In these simulations, preservation probabilities are drawn from a skewed distribution in which there are more intervals of below-average preservation potential than above-average. As expected, episodic preservation yields unbiased estimates of extinction rate and completeness, but also yields a higher variance in these estimates, especially the latter. For example, in simulations involving highly episodic preservation, we may have difficulty deciding whether, say, 50% or 70% of mammalian species are preserved; we can, however, be confident that the figure is much closer to 60% than it is to 10% or 90%.

Preservation probability may vary systematically as well as randomly. For example, there is some evidence that the quality of preservation may increase on long time scales (Raup 1976). The simulation approach is useful for estimating the variance inherent in our estimates of extinction rate and completeness, but the analytic approach presented in Appendix 1 can be modified to accommodate variable preservation probabilities (Appendix 5). Thus, we can predict expected ranges, given an initial distribution of durations and a sequence of preservation probabilities. Several models of variation in preservation probability were explored to determine whether our approach, based on observed ranges, still allows reasonable estimates for extinction rate and completeness in the face of varying preservation (Table 4). In each case, a temporal sequence of 200 preservation probabilities was generated, and 100 successive cohorts of taxa were followed forward for 100 time steps each. Thus the first cohort experiences the first through 100th preservation probabilities, the second experiences the second through 101st, and so on. Most of the taxa in a cohort experience the early preservation probabilities, while few endure long enough to experience the later preservation probabilities. Thus, the average effective preservation probability for a cohort is the mean of the temporal sequence weighted by the fraction of the cohort that survives to a given time. Each cohort was governed by the same underlying extinction rate, which was held constant.

There are two distinct questions to consider. First, for a single cohort, does the temporal variation in preservation probability prohibit accurate estimation of extinction rate and completeness? Second, when all the cohorts are lumped into a single data set, as we have done in the empirical examples above, can the underlying extinction rate and completeness

TABLE 4. Examples of effect of temporal variation in preservation probability on estimates of extinction rate, mean preservation probability, and completeness. Estimates are based on range-frequency distribution for 100 combined cohorts (see text for explanation).

Model	Extinction rate		Mean preservation probability		Completeness	
	Actual	Estimated	Actual	Estimated	Actual	Estimated
Linear increase in preservation probability from 0.0 to 1.0 over 200 time increments	0.25	0.24	0.27	0.23	0.56	0.58
Linear decrease in preservation probability from 1.0 to 0.0 over 200 time increments	0.25	0.24	0.27	0.23	0.56	0.58
Preservation probabilities for time increments drawn randomly from uniform distribution on (0, 1)	0.25	0.25	0.49	0.49	0.82	0.81
Preservation probabilities drawn from skewed (exponential) distribution with mean equal to 0.1	0.25	0.25	0.10	0.093	0.34	0.32
Preservation probability varies sinusoidally from 0.0 to 1.0 with a cycle length of 50 time increments	0.25	0.25	0.50	0.40	0.69	0.76
Preservation probability alternates every time increment between 0.1 and 0.2	0.25	0.25	0.15	0.15	0.45	0.44

be recovered? For example, consider a linear increase in preservation probability. Here, application of Appendix 5 shows that our estimate of extinction rate is biased downward and our estimate of completeness is biased upward for single cohorts. Since both estimates depend on the range-frequency distribution, the biases are not independent. The biases are strongest for cohorts that experience lower preservation probabilities. Intuitively, this can be understood with reference to the nonlinear relationship between preservation probability and completeness illustrated in Figure 6. At low preservation probabilities, there is a substantial change in completeness with just a slight change in preservation probability. However, at higher preservation probabilities, the corresponding change is much smaller. Thus, the effect of averaging different preservation probabilities is much stronger when the probabilities are lower. We have applied Appendix 5 to a number of temporal patterns, including directional, random, and cyclic change in preservation probability (Table 4). Despite the bias within individual cohorts, assembling the data for different cohorts, as we advocate, yields effectively unbiased estimates of extinction rate. There is a bias in estimated completeness in some models, but this is generally small compared to the sam-

pling variance as reflected in the foregoing simulations.

Thus, although our method of estimating extinction rate, preservation probability, and completeness from fossil ranges assumes homogeneous preservation, simulations and analytical calculations suggest that, for sufficiently large data sets on the order of several hundred taxa or more, the method is relatively robust to violations of this assumption.

Discussion and Conclusions

Given any initial distribution of taxonomic durations and any distribution of preservation probabilities, we can predict the observed distribution of fossil ranges. Starting with the assumptions of constant extinction rate (i.e., exponential duration distribution) and random preservation through time and among taxa, we can exactly recover the true extinction rate (hence the original distribution of durations), the preservation probability per unit time, and the proportion of taxa preserved. However, reasonable estimates of these quantities can be obtained even if duration distributions are non-exponential and if preservation potential varies temporally and taxonomically. Because the method requires only observed stratigraphic ranges, not individual occurrences, it should be widely applicable. Cases in which

individual occurrences are available show that the preservation probability estimated from stratigraphic ranges alone allows an accurate prediction of internal gaps within the ranges. Moreover, the finest possible stratigraphic resolution is not needed; even coarsely binned data are appropriate, provided that the length of intervals is not much greater than the median duration of taxa. Given these characteristics, the approach developed here represents a paleobiological tool with great promise.

Currently, the most common approach to estimating original range endpoints from observed ranges is based on calculation of confidence limits on endpoints, which requires knowledge of occurrences within the range of a taxon (Strauss and Sadler 1989; Marshall 1990, 1994b). While such information is potentially powerful, it is generally unavailable in published compilations of stratigraphic ranges. Because the goal of the confidence-limit method of range extensions is to estimate the times of origination and extinction of individual taxa, it treats each taxon separately, rather than as part of a statistical population. The confidence-limit approach is not ideally suited for estimating an original distribution of taxonomic durations, because it considers only those taxa that were actually preserved (cf. Fig. 2B) and, unlike our approach, makes no attempt to recover the durations of taxa that were never preserved. In some ways our approach resembles the model of Pease (1985), but we feel its greater simplicity will make it more widely applicable.

One application of our method shows that the apparent difference in taxonomic longevity between bivalves and mammals is not attributable to a difference in preservation potential. Nevertheless, it must be kept in mind that the methods we describe are statistical in nature. Large data sets are needed, with accurate stratigraphic ranges. Like many analyses of taxonomic data, our approach is potentially sensitive to taxonomic practice. Perhaps most importantly, a reluctance to recognize short-lived or monotypic taxa will tend to reduce the number of taxa confined to a single stratigraphic interval, and thereby inflate estimates of preservation probability and completeness (see Note, Appendix 3). This bias is more likely to present problems at higher taxonomic levels (Raup 1975).

Although many short-ranging taxa may have had truly short durations, a very high frequency of single hits suggests the possibility of a poor fossil record, which should be analyzed with caution. For example, Dodson (1990) summarizes stratigraphic information, at the stage level of resolution, on 285 genera of dinosaurs. Given the high frequency of single hits (83% of the well-dated genera), we advise against taking the distribution of ranges at face value. Moreover, considering how few taxa have ranges of two or more stages, we do not feel confident in estimating preservation probability from the data. In fact, we contend that any analysis of these data will be associated with such a high variance that estimates of duration may be extremely unreliable. For the sake of argument, however, we can compare our estimates of median duration with those of Dodson. In one estimate, Dodson ignores single hits and calculates the median range of the remaining genera. Although superficially similar to our regression-based approach, this does not yield the same estimate of median duration. From various tabulations of the number of genera with ranges of two, three, and four stages (Dodson 1990), our regression method yields estimates of median duration from about 2.5 m.y. to 4.0 m.y., lower than Dodson's estimates (5 m.y. to 10.5 m.y.) based on observed ranges. As shown above (Fig. 9), such a discrepancy is to be expected when stratigraphic intervals are long relative to true median duration.

Estimates of global, species-level completeness for skeletonized taxa have generally been in the range of 10% or less (Newell 1959; Durham 1967; Valentine 1970). Therefore, the estimates presented here may seem rather high. This reflects the distinction between local or regional completeness (most of the data herein) and global completeness (previous work). As Valentine (1989) suggested after finding a high proportion of living molluscan taxa with a Pleistocene fossil record, the incompleteness of the fossil record may reflect the loss of fossiliferous rock more than the initial failure of fossilization. This is also in accord with Schopf's (1978) actualistic study. Our high es-

timates may also reflect our choice of taxa. Trilobites are very well preserved as arthropods go, Paleozoic crinoids are more robust in general than asteroids and holothurians, for example, and it would seem that many mammals have a higher preservation potential than, say, birds. These informal rankings of preservation potential may well be wrong, but the methods we describe here should allow rigorous comparisons of preservability and completeness among major fossil taxa.

In addition to the insight into evolutionary rates and completeness that we have emphasized here, estimates of preservation potential clearly have important implications for genealogical analysis and other evolutionary studies. For example, several recent studies have been concerned with temporal changes in the size of morphological transitions among lineages (e.g., Smith 1994; Wills et al. 1994; Wagner 1995). Because the apparent magnitude of a change in morphology between an ancestor and its ultimate descendant depends on how many intermediates are missing, temporal changes in preservation potential can affect apparent patterns in morphological step size. Huelsenbeck (1994) has explored the effect of preservation probability on the accuracy and resolution of phylogenetic trees. The method of stratocladistics (Bodenbender 1994; Fisher 1994) must assign some weight or credibility to the nonpreservation of taxa where an evolutionary tree would require their existence. Arguments over the probability of finding ancestral taxa in the fossil record hinge upon the completeness of the fossil record (Fortey and Jefferies 1982; Foote 1996). The investigation of these and other questions in evolutionary paleobiology will be strengthened by improved estimates of preservation potential and its role in transforming real to apparent evolutionary patterns. The approaches presented here will be useful in this regard.

Acknowledgments

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Appendix 1

Predicting distribution of observed stratigraphic ranges from original distribution of taxonomic durations

Let T be the original duration of some taxon, let R be the probability that the taxon is preserved at least once in an arbitrary increment of time, and let t be the preserved stratigraphic range (using discrete-time convention; see Fig. 1). If R is stochastically constant through time, the probability that a taxon with original duration T is not preserved at all (i.e., the probability that $t = 0$) is equal to $(1 - R)^T$, and therefore the probability that it is preserved at least once (i.e., the probability that $t \geq 1$) is equal to

$$P_1(T) = 1 - (1 - R)^T. \quad (1)$$

Let there be an arbitrary distribution of taxonomic durations, where $P_D(T)$ is the probability that the duration equals T (strictly speaking, the probability that it is between $T - 1$ and T, since we are dealing with discrete time intervals). For example, with constant extinction rate, q, $P_D(T)$ is equal to $e^{-q(T-1)} - e^{-qT}$ (Fig. 2A). If the probability of preservation is homogeneous among taxa, then the probability that a taxon randomly chosen from this distribution is preserved at least once is equal to

$$P_P = \sum_{T=1}^{\infty} P_1(T)P_D(T). \quad (2)$$

This is, of course, the proportion of taxa preserved (completeness).

We desire a general expression to relate T, t, and R. If the original duration is T and the range, t, is equal to 1, this single occurrence can be in any of T places stratigraphically, and there must be $T - 1$ intervals of non-preservation. Thus, the probability that the range equals 1, given that the duration equals T, is given by

$$P_z(1, T) = TR(1 - R)^{T-1} \quad (3)$$

For ranges greater than unity, there must be $T - t$ instances of non-preservation outside the fossil range, and there must be two instances of preservation at the endpoints; these endpoints

can fall in $(T - t + 1)$ different ways (see Fig. 1). The number of instances of preservation between the endpoints can be anything from zero to $t - 2$, but all the corresponding probabilities sum to unity and so can be ignored. Thus, the probability that the range is equal to t, given that the duration is equal to T, is given by

$$P_z(t, T) = (T - t + 1)R^2(1 - R)^{T-t} \qquad (4)$$

Equations (3) and (4) give the probability that a certain range will be observed, given a particular original duration. We would like to know the probability of a certain range summed over the entire distribution of original durations. Moreover, since we only observe taxa that are preserved, we would like to normalize this expression by the overall probability of being preserved at least once (eq. 2). We thus have the relative frequency of fossil ranges (the probability, for preserved taxa, that the fossil range is equal to t):

$$f(t) = \left[\sum_{T=t}^{\infty} P_z(t, T)P_D(T)\right] \Big/ P_P. \qquad (5)$$

From this expression, we can calculate the mean and median fossil range for some initial distribution of original durations (e.g., Fig. 2C).

From equations (1) and (2), it follows that the probability that a preserved taxon has original duration T, given that it is preserved at least once, is equal to

$$g(T) = P_1(T)P_D(T)/P_P \qquad (6)$$

This expression allows us to calculate the mean and median original duration of taxa that are preserved at least once (e.g., Fig 2B).

Appendix 2

Demonstration that slope of original exponential distribution of durations can be derived from the distribution of fossil ranges

Equations (1)–(5) imply that

$$f(1) = (R/P_P)\left[\sum_{T=1}^{\infty} P_D(T)T(1 - R)^{T-1}\right].$$

Denote the quantity in brackets A. Then

$$f(1) = (R/P_P)A.$$

Similarly,

$$f(2) = (R^2/P_P)\left[\sum_{T=2}^{\infty} P_D(T)(T - 1)(1 - R)^{T-2}\right].$$

Note that, for $T > 1$, $P_D(T) = e^{-q}P_D(T - 1)$. Therefore,

$$f(2) = (e^{-q}R^2/P_P)\left[\sum_{T=2}^{\infty} P_D(T - 1)(T - 1)(1 - R)^{T-2}\right].$$

Clearly, the terms in this series are the same as those in the series A. Therefore, the two sums are equal, and

$$f(2) = (e^{-q}R^2/P_P)A.$$

Similarly,

$$f(3) = (R^2/P_P)\left[\sum_{T=3}^{\infty} P_D(T)(T - 2)(1 - R)^{T-3}\right].$$

Note that, for $T > 2$, $P_D(T) = e^{-2q}P_D(T - 2)$. Therefore,

$$f(3) = (e^{-2q}R^2/P_P)\left[\sum_{T=3}^{\infty} P_D(T - 2)(T - 2)(1 - R)^{T-3}\right].$$

Clearly, the terms in this series are the same as those in the series A. Therefore, the two sums are equal, and

$$f(3) = (e^{-2q}R^2/P_P)A.$$

Likewise,

$$f(4) = (e^{-3q}R^2/P_P)A$$

$$f(5) = (e^{-4q}R^2/P_P)A$$

and so on. Therefore, for $t > 1$,

$$\ln(f(t)) - \ln(f(t + 1)) = q.$$

Since this difference is constant for all values of $t > 1$, the relationship between $\ln(f(t))$ and t is linear for $t > 1$, and the slope of this relationship is equal to $-q$.

Appendix 3

Demonstration that preservation probability (R) can be derived from the distribution of fossil ranges for an initially exponential distribution of durations

From Appendix 2 we have

$$f(1) = (R/P_P)A$$

$$f(2) = (e^{-q}R^2/P_P)A$$

and

$$f(3) = (e^{-2q}R^2/P_P)A.$$

Therefore,

$$\frac{[f(2)^2]}{[f(1)f(3)]} = \frac{e^{-2q}R^4A^2/P_P^2}{(RA)(e^{-2q}R^2A)/P_P^2} = R.$$

Note.—If data fit the exponential model well, one may take advantage of more information on range frequencies, rather than relying solely on f(1), f(2), and f(3). After calculating the regression of $\ln(f(t))$ on t for $t > 1$, one can calculate the predicted values $f'(2)$ and $f'(3)$ and estimate R as

$$R \approx \frac{[f'(2)^2]}{[f(1)f'(3)]}.$$

Note that this should be done only when data fit an exponential distribution well. Otherwise, we recommend using the FreqRat based on the observed values of f(2) and f(3) (see also Appendix 4). It is possible for the FreqRat to exceed unity. In this case, it cannot serve as an estimate of preservation probability. Since we find that single hits predominate and that the FreqRat works for a wide variety of initial duration distributions (see Appendix 4), we suspect that in some cases the FreqRat may be inflated by taxonomists' reluctance to erect taxa with short stratigraphic ranges.

Appendix 4

Demonstration that preservation probability (R) can be approximated from distribution of fossil ranges when initial distribution of durations is not exponential

From Appendix 2 we have

$$f(1) = (R/P_P)\left[\sum_{T=1}^{\infty} P_D(T)T(1 - R)^{T-1}\right]$$

$$f(2) = (R^2/P_P)\left[\sum_{T=2}^{\infty} P_D(T)(T - 1)(1 - R)^{T-2}\right]$$

and

$$f(3) = (R^2/P_P)\left[\sum_{T=3}^{\infty} P_D(T)(T - 2)(1 - R)^{T-3}\right].$$

Using the general rules for multiplying series, we have

$$f(1)f(3) = (R^3/P_P{}^2)\left\{\sum_{i=1}^{\infty}\sum_{j=3}^{\infty}[P_D(i)P_D(j)i(j-2)(1-R)^{i+j-4}]\right\}$$

and

$$f(2)^2 = (R^4/P_P{}^2)\left\{\sum_{i=2}^{\infty}\sum_{j=2}^{\infty}[P_D(i)P_D(j)(i-1)(j-1)(1-R)^{i+j-4}]\right\}.$$

In general, fossil taxa are predominantly those with longer initial durations, especially if R is not very large (Appendix 1). Therefore, we can ignore the first couple of terms in these sums and consider the sums simply from 3 to ∞. Thus,

$$f(1)f(3) \approx (R^3/P_P{}^2)\left\{\sum_{i=3}^{\infty}\sum_{j=3}^{\infty}[P_D(i)P_D(j)i(j-2)(1-R)^{i+j-4}]\right\}$$

and

$$f(2)^2 \approx (R^4/P_P{}^2)\left\{\sum_{i=3}^{\infty}\sum_{j=3}^{\infty}[P_D(i)P_D(j)(i-1)(j-1)(1-R)^{i+j-4}]\right\}.$$

Note that, as i and j increase, the terms $[i(j-2)]$ and $[(i-1)(j-1)]$ progressively approach equivalence. Therefore, the two foregoing double sums are approximately equal, and we have

$$\frac{[f(2)^2]}{[f(1)f(3)]} \approx \frac{R^4P_P{}^2}{R^3P_P{}^2} = R.$$

Appendix 5

Predicting distribution of observed stratigraphic ranges from original distribution of taxonomic durations when preservation probability varies over time

Let R_i be the probability of preservation in the ith time interval. For convenience, we can number time intervals so that R_1 is the preservation probability during the first interval of a taxon's existence, and so on. Then, the probability that a taxon with duration T is preserved at least once is equal to

$$P_1(T) = 1 - \prod_{i=1}^{T}(1 - R_i). \qquad (7)$$

Thus, the proportion of lineages preserved is equal to

$$P_P = \sum_{T=1}^{\infty} P_D(T)\left[1 - \prod_{i=1}^{T}(1 - R_i)\right]. \qquad (8)$$

If a lineage is preserved as a single hit, this can be in any of T intervals. The probability of preservation in only one interval is equal to

$$P_z(1,T) = \sum_{j=1}^{T}\left\{\left[\prod_{i=1}^{j-1}(1-R_i)\right]R_j\left[\prod_{i=j+1}^{T}(1-R_i)\right]\right\}. \qquad (9)$$

The index of the sum refers to the fact that the one instance of preservation can occur in T possible intervals. The first term in the sum reflects the prior instances of nonpreservation, the middle term reflects the one instance of preservation, and the last term reflects the subsequent intervals of nonpreservation. Similarly, for ranges of two or more intervals, the probability of a given range is equal to

$$P_z(t,T) = \sum_{j=1}^{T-t+1}\left\{\left[\prod_{i=1}^{j-1}(1-R_i)\right]R_jR_{j+t-1}\left[\prod_{i=j+t}^{T}(1-R_i)\right]\right\}. \qquad (10)$$

Here, the index of the sum reflects the fact that the range endpoints can occur in $T - t + 1$ places. The first term and last term again reflect prior and subsequent instances of nonpreservation, and the two middle terms reflect preservation in the first and last intervals of the taxon's range. Given these expressions for P_P and $P_z(t,T)$, the frequency of observed taxon ranges can be calculated using equation (5) (Appendix 1).

Appendix 6

Probability of paraclade preservation if species-level preservation probability (R), origination rate (p), and extinction rate (q) are stochastically constant

Assume that the paraclade is initially monotypic. Let $P_{0,T}$ denote the probability of paraclade extinction at or before time T (see Raup 1985: eqs. A11 and A13). Then the probability that the paraclade duration is equal to T, i.e., that extinction occurs during the Tth time increment, is equal to

$$P_D(T) = P_{0,T} - P_{0,T-1}$$

Let $P_{n,x}$ denote the probability that paraclade diversity at time x is equal to n lineages (see Raup 1985: eqs. A15 and A17). Let $(P_{0,T}|n,x)$ denote the probability of paraclade extinction at or before time T given that diversity is equal to n at time $x < T$. Then

$$(P_{0,T}|n,x) = [P_{0,T-x}]^n \qquad \text{(see Raup 1985: eqs. A12 and A14).}$$

Let $(P_D(T)|n,x)$ denote the probability that paraclade extinction occurs during the Tth time step, given that diversity is equal to n at time $x < T$. Then

$$(P_D(T)|n,x) = [P_{0,T-x}]^n - [P_{0,T-x-1}]^n$$

Let $(P_D(T),n,x)$ denote the probability that diversity is equal to n at time $x < T$ *and* that paraclade extinction occurs during the Tth time increment. Then

$$(P_D(T),n,x) = (P_D(T)|n,x)P_{n,x}$$

Let $(P_{n,x}|D = T)$ denote the probability that diversity is equal to n at time $x < T$, given that paraclade extinction occurs during the Tth time step. Then

$$(P_{n,x}|D = T) = (P_D(T), n, x)/P_D(T)$$

Finally, let $R(x,T)$ denote the probability that at least one lineage of a paraclade is preserved during the xth time increment, given that the ultimate paraclade duration is equal to T. If the paraclade has n lineages each with the same preservation probability R, then the probability that none of them is preserved is equal to $(1 - R)^n$, and the probability that at least one of them is preserved is equal to $1 - (1 - R)^n$. These expressions are then weighted by the probability that the paraclade has n lineages, where n varies from 1 to ∞, and we have

$$R(x, T) = \sum_{n=1}^{\infty}\{(P_{n,x}|D = T)[1 - (1 - R)^n]\}.$$

To determine the expected distribution of stratigraphic ranges of fossil paraclades, $R(x,T)$ is simply substituted for R_i in equations (7)–(10) (Appendix 5), making the appropriate substitutions from Raup (1985: eqs. A11–A17) cited above. Clearly, the expression for $R(x,T)$ can easily be modified to accommodate taxonomic and temporal variation in the species-level preservation probability (R), although we do not present these results here.