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ARTICLES

Origination and Extinction through the Phanerozoic: A New Approach

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ABSTRACT

Temporal patterns of origination and extinction are essential components of many paleontological studies, but it has been difficult to obtain accurate rate estimates because the observed record of first and last appearances is distorted by the incompleteness of the fossil record. Here I analyze observed first and last appearances of marine animal and microfossil genera in a way that explicitly takes incompleteness and its variation into consideration. This approach allows estimates of true rates of origination and extinction throughout the Phanerozoic. Substantial support is provided for the proposition that most rate peaks in the raw data are real in the sense that they do not arise as a consequence of temporal variability in the overall quality of the fossil record. Even though the existence of rate anomalies is supported, their timing is nevertheless open to question in many cases. If one assumes that rates of origination and extinction are constant through a given stratigraphic interval, then peaks in revised origination rates tend to be displaced backward and extinction peaks forward relative to the peaks in the raw data. If, however, one assumes a model of pulsed turnover, with true originations concentrated at lower interval boundaries and true extinctions concentrated at upper interval boundaries, the apparent timing of extinction peaks is largely reliable at face value. Thus, whereas rate anomalies may well be real, precisely when they occurred is a question that cannot be answered definitively without independent support for a model of smooth versus pulsed rate variation. The pattern of extinction, particularly the major events, is more faithfully represented in the fossil record than that of origination. There is a tendency for the major extinction events to occur during stages in which the quality of the record is relatively high and for recoveries from extinctions to occur when the record is less complete. These results imply that interpretations of origination and extinction history that depend only on the existence of rate anomalies are fairly robust, whereas interpretations of the timing of events and the temporal covariation between origination and extinction may require substantial revision.

Origination and Extinction in Earth History

Quantitative analysis of the stratigraphic ranges of fossil taxa has revealed striking patterns in the history of life on Earth, particularly during the Phanerozoic Eon. At the most overarching scale, there has been a secular decline in the average rate of appearance of new species, genera, and families and in the disappearance of existing taxa since the Early Cambrian (Raup and Sepkoski 1982; Van Valen 1984; Gilinsky and Bambach 1987). With respect to the overall statistical relationship between origination and extinction, peak rates of first appearance tend to lag peak rates of last appearance by several million years (Kirchner and Weil 2000*b*). There is also evidence that changes in observed biological diversity are more strongly linked to extinction than origination during the Paleozoic era, whereas origination plays a stronger role in diversity variation during the Mesozoic and Cenozoic eras (Foote 2000*a*). Numerous other examples could be cited. What these cases have in common is, first, that they reflect some of the largest-scale features that one sees when studying the fossil record and, second, that their explanations, which are yet to be found, are potentially of great geological and biological importance.

A third factor that these and many other studies have in common is that, faute de mieux, they take observed times of first and last appearance as rea-

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sonable approximations for true times of origination and extinction. We know, however, that this approximation is suspect and that apparent rates of taxonomic evolution are distorted by incompleteness of the fossil record in general and by variable completeness in particular. For example, if many species become extinct at essentially the same time, their last appearances will be smeared out downsection. Thus, the apparent rate of extinction will be spuriously high leading up to the true event and spuriously low at the event itself. First appearances are likewise smeared forward in time. Moreover, times when the quality of sampling is unusually high tend to have spuriously high apparent rates of origination and extinction and to be flanked by intervals with spuriously low rates. A converse effect is expected when sampling is unusually poor.

Although these and related problems have long been recognized (Darwin [1859] 1964; Signor and Lipps 1982; Koch 1991; MacLeod and Keller 1991), some recent developments call for a comprehensive reevaluation of origination and extinction rates. Many analyses have been drawing biological insight from the relationship between origination and extinction patterns (Stanley 1990; Hallam 1991; Erwin 1998; Foote 2000*b*; Kirchner and Weil 2000*a*, 2000*b*; Plotnick and Sepkoski 2001; Kirchner 2002), but a number of empirical studies have cast doubt on these results by suggesting that apparent taxonomic rates are higher when there is more preserved sedimentary rock, just as one would expect if temporal variation in rates were largely spurious (Smith 2001; Peters and Foote 2002). Moreover, modeling of sequence stratigraphy suggests that spurious variation in patterns of first and last appearance may be quite common in general (Holland 1995, 2000; Holland and Patzkowsky 2002), and particular events have been called into question on these grounds (Smith et al. 2001). Finally, empirical estimates of the amount of preserved sedimentary rock have been combined with mathematical models that predict expected patterns of first and last appearance from true rates of biotic turnover and preservation (Peters and Foote 2002). This modeling shows that, in a broad statistical sense, the apparent pattern of extinction in the marine realm would look very much like the empirical record if true taxonomic rates had in fact been constant during the past half-billion years.

This last result admits at least two plausible interpretations. First, the apparent variation in rates may be largely an artifact of variation in the record. Second, true extinction rates and the quality of the record may share a latent cause. Distinguishing between these alternatives and understanding life's history on Earth more generally clearly require that we obtain accurate estimates of origination and extinction rates. The goal of this article is to develop such estimates, paying special attention to the reality and timing of observed rate peaks. The question of timing is addressed here at a relatively coarse level; the goal is to identify the stratigraphic interval or intervals, if any, during which rates were elevated. As these intervals are on the order of a few million years long, this work has nothing to say about whether events such as the end-Paleozoic extinction were spread out over some 10^5 years (Bowring et al. 1998) or substantially longer (Metcalfe et al. 2001; Mundil et al. 2001).

Recalibrating Taxonomic Rates

I have analyzed Sepkoski's (1996, 2002) data on the stratigraphic ranges of marine animal and microfossil genera, using an approach (Foote 2001*b*) that simultaneously estimates origination, extinction, and preservation rates from recorded times of first and last appearance. Detailed data on occurrences within stratigraphic ranges are not yet available for the entire Phanerozoic, so the approach of sampling standardization (Alroy 1996, 1998) cannot yet be applied at this scale. Moreover, making sampling uniform, though it may alleviate problems that stem from variable completeness, still leaves the distorting effects of general incompleteness (Foote 2001*b*). The Phanerozoic was subdivided into 77 conventional stratigraphic intervals, mostly stages and substages, with an average estimated duration of 7.1 m.yr. on the basis of the time scale of Golonka and Kiessling (2002), with modifications following Bowring and Erwin (1998). Stratigraphic terminology follows Sepkoski. All told, I used 31,061 genera whose first and last appearances could be adequately resolved. A summary of first and last appearances is given in table 3, available on request from the Data Depository of *The Journal of Geology*. Results obtained with Sepkoski's (1992) family-level data are similar to those found with genera and are therefore not presented here.

In brief, the approach used here starts with forward modeling of the expected pattern of preserved first and last appearances corresponding to a given evolutionary model and a specified sequence of true rates of origination, extinction, and preservation (including sampling). It then uses numerical optimization to find the best-fitting set of rates, that is, the rates that predict a pattern of first and last appearances in maximal agreement with those actually observed in the fossil record.

This approach is similar to capture-recapture methods that have been adopted from population biology and applied to paleontological data with the express purpose of taking incomplete sampling into consideration (Nichols and Pollock 1983; Conroy and Nichols 1984; Nichols et al. 1986; Niklas and Tiffney 1994; Connolly and Miller 2001*a*, 2001*b*, 2002). The first occurrence of a taxon in the fossil record is analogous to the initial capture and marking of the individual in an animal population, and subsequent occurrences are analogous to subsequent encounters of marked individuals. Numerous models and statistical procedures have been developed to estimate rates of encounter (i.e., preservation and sampling when applied to paleontological data), birth or immigration (i.e., origination), and death or emigration (i.e., extinction) (Brownie et al. 1985; Burnham et al. 1987; Pollock et al. 1990; Pradel 1996; Nichols et al. 2000). The various models make different assumptions about the structure of populations and the nature of the data. Two points are of particular importance for paleontological applications.

First, capture-recapture models typically assume that there is the potential for multiple encounters in the data, for example, in successive seasons or years. Band-recovery models, however, assume that an individual is banded and then encountered only once subsequently, when it is killed (Brownie et al. 1985). The initial paleontological applications of capture-recapture methods focused mainly on band-recovery models, since large-scale taxonomic compilations typically consist of only first and last occurrences of fossil taxa (Nichols and Pollock 1983; Conroy and Nichols 1984; Nichols et al. 1986). More recently, capture-recapture models with multiple encounters have been exploited to estimate origination, extinction, and sampling rates from intensively collected data consisting of multiple occurrences within the stratigraphic ranges of taxa (Connolly and Miller 2001*a*, 2001*b*, 2002). Such comprehensive data are not yet available for the entire Phanerozoic, however. Methods that estimate origination, extinction, and sampling rates from first and last occurrences are therefore needed.

Second, the models used in capture-recapture studies generally assume relatively brief time intervals during which individuals are encountered, separated by longer intervals during which birth, death, and migration take place. As Nichols and Pollock (1983) recognized, paleontological data consisting of the numbers of first and last occurrences during a sequence of long stratigraphic intervals violate this assumption. The importance of this violation can be assessed by experimenting with different degrees of stratigraphic resolution (Connolly and Miller 2001*b*). Alternatively, one can develop models that explicitly account for the extensive origination and extinction that take place within time intervals. This is the approach adopted herein.

Details of Method

The method assumes that each operational stratigraphic interval, such as the stage, is characterized by its own rate of origination, extinction, and preservation. These rates are free to vary from stage to stage, but all taxa within a stage are assumed to be governed by the same rates. Observed data are cast in the form of a first-last appearance matrix $\mathbf{X}$, where X_{ij} is the number of genera with first appearance in stage i and last appearance in stage j. The observed forward survivorship frequency, $F_{\rightarrow ij}$, is defined as the proportion of genera first appearing in stage i that have last appearance in stage j, i.e.,

$$F_{\rightarrow ij} = \frac{X_{ij}}{\sum_{k=i}^{n} X_{ik}}.$$

Similarly, the observed backward survivorship frequency, $F_{\leftarrow ij}$, is the proportion of genera last appearing in stage j that have first appearance in stage i, i.e.,

$$F_{\leftarrow ij} = \frac{X_{ij}}{\sum_{k=1}^{j} X_{kj}}.$$

Evolutionary Models. Two end-member models of taxonomic turnover were considered. The continuous turnover model assumes that per capita rates of origination and extinction are constant throughout a given stratigraphic interval. The pulsed turnover model, by contrast, assumes that all turnover occurs at interval boundaries, with originations clustered at the beginning of an interval and extinctions clustered at the end. The relative merits of these models will be touched on later, but it can fairly be said that neither model is known to hold more generally than the other. Hybrid models (continuous origination with pulsed extinction and vice versa) yield rate estimates nearly identical to those obtained using end-member models (results not presented). A model in which turnover is pulsed but there are numerous pulses within a single interval (Raup 1991) is essentially the same as the continuous turnover model.

The different models of turnover have important implications for preservation. If extinctions are spread throughout a stage, genera that truly become extinct during a given stage span less of that stage than they would if they all persisted to its end. It is therefore easier for a genus to escape preservation during its stage of true extinction under the continuous turnover model than under the pulsed turnover model; in other words, it is easier for a true extinction in a given stage to be represented as a last appearance in the previous stage. Similar reasoning holds for origination.

There is yet another layer to this interplay between assumed evolutionary model and implied pattern of preservation. To attribute a large proportion of last appearances in a given stage to a true extinction event in that stage requires better sampling and/or a higher true extinction rate within that stage if one assumes constant as opposed to pulsed extinction. This again is because genera that become extinct during a particular stage span less of that stage in reality if extinction is constant through the stage than if it is concentrated at the end.

Forward and Backward Survivorship Probabilities. Because the goal is to infer rates from an incomplete fossil record, the probabilities of interest concern preserved patterns of first and last appearance rather than true times of origination and extinction. For simplicity, I will refer to these as survivorship probabilities.

The model in which origination and extinction rate are assumed constant within a time interval has already been considered (Foote 2001*b*). In addition to generalizing the survivorship probabilities to allow for rates that are constant, pulsed, or mixed, this section simplifies the previous expression for the proportion of taxa confined to their interval of first or last appearance. Here, pulsed origination is assumed to be concentrated at the beginning of the time interval. Thus, all taxa that truly exist during a specified interval, whether they originate during that interval or carry over from the prior interval, are necessarily extant at the start. This is the case whether extinction is assumed to be continuous or pulsed. Likewise, pulsed extinction is assumed to be concentrated at the end of the interval, with the effect that, regardless of the origination model, any taxon that exists during an interval is extant at the end of that interval.

$P_{\rightarrow ij}$ is the forward survivorship probability, i.e., the probability that a taxon will have last appearance in interval j, given that its first appearance is in interval i; $P_{\leftarrow ij}$ is the analogous backward survivorship probability. For a given interval of time, let X_{bL}, X_{Ft}, X_{FL}, and X_{bt} be the observed numbers of taxa, respectively, that cross the bottom boundary and last appear within the interval, that first appear within the interval and cross its top boundary, that have both first and last appearance during the interval, and that range through the interval, crossing both the bottom and top boundaries. N_{bL}, N_{Ft}, N_{FL}, and N_{bt} are the corresponding true numbers of taxa (Foote 2000*a*).

Although a more complicated derivation was presented previously (Foote 2001*b*), $P_{\rightarrow ii}$, the probability of being a single-interval taxon, given first appearance in interval i, can be expressed simply as the number of singletons divided by the total number of first appearances, $X_{\mathrm{FL}}/(X_{\mathrm{Ft}} + X_{\mathrm{FL}})$. Similarly, $P_{\leftarrow jj} = X_{\mathrm{FL}}/(X_{\mathrm{bL}} + X_{\mathrm{FL}})$. The expressions for the X values depend on the true numbers N_{bL} and so forth and on the probabilities of preservation before, during, and after the interval in question. P_{B} is the probability of preservation sometime before an interval, given that a taxon is extant at the start of the interval. P_{A} is the probability of preservation sometime after an interval, given that a taxon is extant at the end of the interval. $P_{\mathrm{D|bL}}$, $P_{\mathrm{D|Ft}}$, $P_{\mathrm{D|FL}}$, and $P_{\mathrm{D|bt}}$ are the probabilities of preservation during the interval, given that the taxon truly belongs in the category N_{bL}, N_{Ft}, N_{FL}, or N_{bt}, respectively. When necessary to distinguish values for particular intervals, these quantities are denoted in the manner of $P_{\mathrm{B}}(i)$ for interval i and so on. The origination, extinction, and preservation rates for interval i are denoted p_i, q_i, and r_i, and the intervals are numbered from $i = 1$ to $i = n$, where n is the number of intervals.

Under the assumption of continuous turnover within a stage, p and q are per capita rates per taxon per stage (Foote 2000*a*). Rates are expressed per stage rather than per millions of years in order to facilitate comparison between the continuous and pulsed models; for calculations to be dimensionally correct, there is a unit time term implied. Under the assumption of pulsed turnover, p is the factor by which the starting diversity N_{b} (equal to $N_{\mathrm{bL}} + N_{\mathrm{bt}}$) needs to be multiplied to yield the total number of new lineages in the interval. Thus, the total diversity for an interval is equal to the starting diversity multiplied by $1 + p$. Because diversity can more than double, p is not strictly a probability per starting taxon. Under the pulsed-extinction model, q is the probability that a taxon extant during the interval will become extinct during the interval.

As previously discussed (Foote 2000*a*), the X values for a given interval are determined as follows:

$$X_{\mathrm{bL}} = N_{\mathrm{bL}}P_{\mathrm{B}}P_{\mathrm{D|bL}} + N_{\mathrm{bt}}P_{\mathrm{B}}P_{\mathrm{D|bt}}(1 - P_{\mathrm{A}}), \tag{1}$$

$$X_{\mathrm{Ft}} = N_{\mathrm{Ft}}P_{\mathrm{A}}P_{\mathrm{D|Ft}} + N_{\mathrm{bt}}P_{\mathrm{A}}P_{\mathrm{D|bt}}(1 - P_{\mathrm{B}}), \tag{2}$$

$$\begin{aligned} X_{\mathrm{FL}} = {} & N_{\mathrm{FL}}P_{\mathrm{D|FL}} + N_{\mathrm{bL}}(1 - P_{\mathrm{B}})P_{\mathrm{D|bL}} \\ & + N_{\mathrm{Ft}}(1 - P_{\mathrm{A}})P_{\mathrm{D|Ft}} + N_{\mathrm{bt}}(1 - P_{\mathrm{B}})P_{\mathrm{D|bt}}(1 - P_{\mathrm{A}}), \end{aligned} \tag{3}$$

$$X_{\mathrm{bt}} = N_{\mathrm{bt}}P_{\mathrm{B}}P_{\mathrm{A}}. \tag{4}$$

The relevant expressions under the different models are presented, with explanatory notes, in table 1.

Once the expression for $P_{\rightarrow ii}$ is in hand, determining the remaining forward survivorship probabilities rests on the fact that the probability of truly surviving to the end of an interval, if extant at the start, is equal to e^{-q} if extinction is continuous and to $1 - q$ if extinction is pulsed. Thus, the corresponding probabilities of becoming extinct during the interval are equal to $1 - e^{-q}$ and q. Similarly, starting with $P_{\leftarrow jj}$, the remaining backward survivorship probabilities use the fact that the probability of being extant at the start of an interval, if extant at the end, is equal to e^{-p} if origination is continuous and to $1/(1 + p)$ if origination is pulsed. The corresponding probabilities of origination are therefore $1 - e^{-p}$ and $p/(1 + p)$. To have a last appearance in interval j, given first appearance in interval i $(j > i)$, a taxon must survive at least to the end of interval $j - 1$; the probability of surviving at least this long is equal to $e^{-\Sigma_{k=i+1}^{j-1} q_k}$ for continuous extinction and to $\prod_{k=i+1}^{j-1}(1 - q_k)$ for pulsed extinction. To appear last in interval j, either the taxon can become extinct in j and be preserved therein, with probability $(1 - e^{-q_j})P_{\mathrm{D|bL}}(j)$ or $q_jP_{\mathrm{D|bL}}(j)$, or it can survive to the end of j, be preserved therein, and not be preserved thereafter, with probability $(e^{-q_j})P_{\mathrm{D|bt}}(j)[1 - P_{\mathrm{A}}(j)]$ or $(1 - q_j)P_{\mathrm{D|bt}}(j)[1 - P_{\mathrm{A}}(j)]$. Thus,

$$P_{\rightarrow ij} = \frac{[(1 - P_{\rightarrow ii})e^{-\Sigma_{k=i+1}^{j-1} q_k}]\{(1 - e^{-q_j})P_{\mathrm{D|bL}}(j) + e^{-q_j}P_{\mathrm{D|bt}}(j)[1 - P_{\mathrm{A}}(j)]\}}{P_{\mathrm{A}}(i)}, \tag{5a}$$

or

$$P_{\rightarrow ij} = \frac{(1 - P_{\rightarrow ii})[\prod_{k=i+1}^{j-1}(1 - q_k)]\{q_jP_{\mathrm{D|bL}}(j) + (1 - q_j)P_{\mathrm{D|bt}}[1 - P_{\mathrm{A}}(j)]\}}{P_{\mathrm{A}}(i)}, \tag{5b}$$

depending on whether extinction is continuous or pulsed. The division by $P_{\mathrm{A}}(i)$ is necessary to condition the probability on the taxon's occurring sometime after interval i.

The same reasoning leads to the following expressions for backward survivorship:

$$P_{\leftarrow ij} = \frac{[(1 - P_{\leftarrow jj})e^{-\Sigma_{k=i+1}^{j-1} p_k}]\{(1 - e^{-p_i})P_{\mathrm{D|Ft}}(i) + e^{-p_i}P_{\mathrm{D|bt}}(i)[1 - P_{\mathrm{B}}(i)]\}}{P_{\mathrm{B}}(j)}, \tag{6a}$$

or

$$P_{\leftarrow ij} = \frac{(1 - P_{\leftarrow jj})[\prod_{k=i+1}^{j-1} 1/(1 + p_k)]\{p_i/(1 + p_i)P_{\mathrm{D|Ft}}(i) + 1/(1 + p_i)P_{\mathrm{D|bt}}(i)[1 - P_{\mathrm{B}}(i)]\}}{P_{\mathrm{B}}(j)}, \tag{6b}$$

for continuous and pulsed origination, respectively.

Optimization Procedure. The best-fitting rates are found by numerically minimizing the sum of log deviations between $F_{\rightarrow ij}$ and $P_{\rightarrow ij}$ and between $F_{\leftarrow ij}$ and $P_{\leftarrow ij}$, weighted by the corresponding observed number of genera:

$$\sum_{i=1}^{n}\sum_{j=i}^{n} X_{ij}\left|\ln\left(\frac{P_{\rightarrow ij}}{F_{\rightarrow ij}}\right)\right| + \sum_{j=1}^{n}\sum_{i=1}^{j} X_{ij}\left|\ln\left(\frac{P_{\leftarrow ij}}{F_{\leftarrow ij}}\right)\right|.$$

This approach assigns equal weight to each genus. All told, 230 parameters are estimated from the data: namely, origination, extinction, and preservation rates for each of 76 pre-Holocene time intervals, plus initial and final preservation probabilities $P_{\mathrm{B}}(1)$ and $P_{\mathrm{A}}(n)$. All parameters are estimated simultaneously; thus, each parameter takes on a fixed value for a given stage and must satisfy constraints of both forward and backward survivorship.

As described previously (Foote 2001*b*), the method of simulated annealing (Press et al. 1992) is used to explore the parameter space without becoming trapped on local optima. For a given set of first and last occurrences, there are innumerable

Table 1. Expressions Used to Calculate Survivorship Probabilities

Quantity/model	Expression
N_{bt}:	
••C	$N_{\mathrm{b}}e^{-q}$
•P	$N_{\mathrm{b}}(1-q)$
N_{bL}:	
•C	$N_{\mathrm{b}}(1-e^{-q})$
•P	$N_{\mathrm{b}}q$
N_{Ft}:	
CC	$N_{\mathrm{b}}e^{p-q}(1-e^{-q})$
PP	$N_{\mathrm{b}}p(1-q)$
CP	$N_{\mathrm{b}}e^{p}(1-q)(1-e^{-p})$
PC	$N_{\mathrm{b}}pe^{-q}$
N_{FL}:	
CC[a]	$N_{\mathrm{b}}(e^{-q}+p-1)$ if $p=q$, $N_{\mathrm{b}}\dfrac{qe^{(p-q)}+(p-q)e^{-q}-p}{p-q}$ if $p\neq q$
PP	$N_{\mathrm{b}}pq$
CP	$N_{\mathrm{b}}q(e^{p}-1)$
PC	$N_{\mathrm{b}}p(1-e^{-q})$
$P_{\mathrm{A}}(i)$:	
•C	$\sum_{k=i+1}^{n}\left(\left[\left(e^{-\Sigma_{m=i+1}^{k}q_m}\right)(1-e^{-q_k})\right]\left\{1-\left(e^{-\Sigma_{m=i+1}^{k-1}r_m}\right)[1-P_{\mathrm{D\|bL}}(k)]\right\}\right)+\left(e^{-\Sigma_{k=i+1}^{n}q_k}\right)\left\{1-\left(e^{-\Sigma_{k=i+1}^{n}r_k}\right)[1-P_{\mathrm{A}}(n)]\right\}$
•P	$\sum_{k=i+1}^{n}\left(\left(\prod_{m=i+1}^{k}1-q_m\right)(q_k)\left\{1-\left(e^{-\Sigma_{m=i+1}^{k-1}r_m}\right)[1-P_{\mathrm{D\|bL}}(k)]\right\}\right)+\left[\prod_{k=i+1}^{n}(1-q_k)\right]\left\{1-\left(e^{-\Sigma_{k=i+1}^{n}r_k}\right)[1-P_{\mathrm{A}}(n)]\right\}$
$P_{\mathrm{B}}(i)$:	
C•	$\sum_{k=1}^{i-1}\left(\left[\left(e^{-\Sigma_{m=k}^{i-1}p_m}\right)(1-e^{-p_k})\right]\left\{1-\left(e^{-\Sigma_{m=k+1}^{i-1}r_m}\right)[1-P_{\mathrm{D\|Ft}}(k)]\right\}\right)+\left(e^{-\Sigma_{k=1}^{i-1}p_k}\right)\left\{1-\left(e^{-\Sigma_{k=1}^{i-1}r_k}\right)[1-P_{\mathrm{B}}(1)]\right\}$
P•	$\sum_{k=1}^{i-1}\left(\left(\prod_{m=k}^{i-1}\frac{1}{1+p_m}\right)\left(\frac{p_k}{1+p_k}\right)\left\{1-\left(e^{-\Sigma_{m=k+1}^{i-1}r_m}\right)[1-P_{\mathrm{D\|Ft}}(k)]\right\}\right)+\left(\prod_{k=1}^{i-1}\frac{1}{1+p_k}\right)\left\{1-\left(e^{-\Sigma_{k=1}^{i-1}r_k}\right)[1-P_{\mathrm{B}}(1)]\right\}$
$P_{\mathrm{D\|bt}}$:	
••	e^{-r}
$P_{\mathrm{D\|bL}}$:	
•C[b]	$\dfrac{[r+qe^{-(q+r)}]/(q+r)-e^{-q}}{1-e^{-q}}$
•P	e^{-r}
$P_{\mathrm{D\|Ft}}$:	
C•[c]	$\dfrac{[r+pe^{-(p+r)}]/(p+r)-e^{-p}}{1-e^{-p}}$
P•	e^{-r}
$P_{\mathrm{D\|FL}}$:	
CC[d]	$\dfrac{N_{\mathrm{b}}p}{N_{\mathrm{FL}}}\left\{\dfrac{r}{p+r}-\dfrac{1-e^{-p}}{p}-\dfrac{p[1-e^{-(p+r)}]}{(p+r)^2}\right\}$ if $p=q$, $\dfrac{N_{\mathrm{b}}}{N_{\mathrm{FL}}}\left\{\dfrac{pr[e^{(p-q)}-1]}{(q+r)(p-q)}+\dfrac{pqe^{-(q+r)}[e^{(p+r)}-1]}{(p+r)(q+r)}-e^{-q}(e^{p}-1)\right\}$ if $p\neq q$
PP	e^{-r}
CP[e]	$\dfrac{r(e^{p}-1)+p(e^{-r}-1)}{p(r+p)(e^{p}-1)}$
PC[f]	$\dfrac{r(e^{q}-1)+q(e^{-r}-1)}{q(r+q)(e^{q}-1)}$

Note. In the two-character code for model, the first character denotes origination and the second extinction; C = continuous, P = pulsed. A bullet means the expression applies to either model for the corresponding process. N_b is the true standing diversity at the start of the interval; because all relevant numbers scale to N_b, this can be arbitrarily set to unity.

[a] Foote 2000*a*, eqq. (6b) and (6c).

[b] Foote 2000*a*, eq. (27b).

[c] Foote 2000*a*, eq. (28b).

[d] Foote 2000*a*, eqq. (29b) and (29c).

[e] Let z represent time within an interval of duration t, where $z=0$ and $z=t$ are the beginning and end of the interval, respectively. By assumption, there is no extinction until the end of the interval. Thus, the density of origination at time z is equal to $e^{pz}/(e^{pt}-1)$ (cf. Foote 2001*a*, eq. [3]). Because all lineages originating within the interval extend to the end, the probability of preservation, given origin at z and extinction at t, is equal to $1-e^{-r(t-z)}$. It is necessary to integrate the density of origination times the probability of preservation over all values of z. Thus, $P_{\mathrm{D\|FL}}=[1/(e^{pt}-1)]\int_0^t e^{pz}[1-e^{-r(t-z)}]dz$, which is equal to the expression in the table once t is set to unity.

[f] Derived as in the foregoing footnote, with origination and extinction reversed.

solutions that fit essentially equally well. When multiple solutions are inspected, the log deviation varies within narrow bounds, having a standard deviation typically around 1% of the mean value. Thus, the search procedure is unlikely to be settling for local optima that are far from the global optimum. This result, which is analogous to the existence of the numerous, equal-length evolutionary trees that commonly result from a phylogenetic analysis, does not represent a flaw in the method but rather reflects the fact that alternative parameter sets really are indistinguishably good at explaining the observed data. The reasonable fit between model and data supports this interpretation.

In addition to the uncertainty in parameter estimates associated with the optimization procedure, there is variance in the data that must be taken into consideration. This is done by bootstrap resampling, where the fundamental sampling unit is the stratigraphic range of a genus. The optimization is performed 100 times, each time with a different bootstrap sample. The mean parameter values from these optimizations are considered the best-fit rate estimates, and the standard deviation around each mean measures the uncertainty in the corresponding rate estimate. The optimization algorithm must be "tuned" for a given problem (Press et al. 1992). This was done in such a way that further varying the relevant variables of the algorithm, with a consequent increase in computational effort, yielded a negligible (<1%) decrease in the mean log deviation and in the standard deviation about this mean.

In a previous application of this approach (Foote 2001*b*), I minimized the quantity

$$\sum_{i=1}^{n}\sum_{j=i}^{n}\left|\ln\left(\frac{P_{\rightarrow ij}}{F_{\rightarrow ij}}\right)\right| + \sum_{j=1}^{n}\sum_{i=1}^{j}\left|\ln\left(\frac{P_{\leftarrow ij}}{F_{\leftarrow ij}}\right)\right|,$$

a procedure that gives equal weight to each nonzero value of $F_{\rightarrow ij}$ and $F_{\leftarrow ij}$ rather than to each genus. With simulated data that conform to the assumed evolutionary model, both procedures yield accurate parameter estimates (results not presented). There are two potential advantages of the procedure employed here, however. First, there is a theoretical expectation (Kendall 1948; Raup 1978) that older genera should have a lower probability of extinction than younger genera at any given time, and there is also empirical evidence in support of this expectation (Raup 1978; Foote 2001*a*; but see Van Valen 1994 for a contrary interpretation). Similar age dependencies may also exist for origination rates (Foote 2001*a*). The optimization procedure that gives equal weight to each value of $F_{\rightarrow ij}$ and $F_{\leftarrow ij}$ will in essence be forced to compromise between estimating higher rates for younger genera and lower rates for older genera. The approach adopted here lets genera of a given age contribute to the solution in proportion to their actual numbers, thereby reducing the difficulties posed by the heterogeneity in the data. Second, and consequently, this procedure yields parameter estimates with smaller uncertainties. Nevertheless, for the data analyzed here, parameter estimates are generally similar with either procedure (results not presented). Thus, although the weighting protocol adopted here is preferable, the conclusions drawn in this article do not hinge on this protocol.

Taxonomic Rates for Phanerozoic Marine Genera

Raw Data. Figures 1 and 2 show rates of apparent origination and extinction, assuming that first and last appearances are equivalent to originations and extinctions. The origination and extinction profiles show many familiar features, such as a secular decline (Raup and Sepkoski 1982; Van Valen 1984; Gilinsky and Bambach 1987) and numerous peaks superimposed on background levels (Sepkoski 1986, 1996, 1997, 1998). Some variation in rates can be attributed to stage length (Foote 1994, 2000*a*), but the temporal patterns of figures 1 and 2 are largely the same if rates are expressed as per m.yr. rather than per stage (results not presented).

Revised Turnover Rates. Revised rates of origination and extinction (figs. 3, 4) are not constant over the Phanerozoic; evidently, many peaks cannot be dismissed as artifacts of variability in the quality of the fossil record. This immediately suggests that the agreement between observed extinction rates and those expected on the basis of variability in the record (Peters and Foote 2002) may reflect a common latent cause affecting true extinction rates and the stratigraphic record, rather than a direct influence of stratigraphic variation on apparent rates of extinction. Because major turnover events are not simply times of apparent origination and extinction but often mark substantial qualitative changes in faunal composition (Sepkoski 1981, 1984; Droser et al. 2000), it is perhaps not surprising that apparent rate peaks seem to be robust.

Preservation Rates. As discussed above, the continuous turnover model is expected to yield higher estimates of preservation rate than the pulsed model for intervals with high origination or extinction rates. This expectation is largely borne out

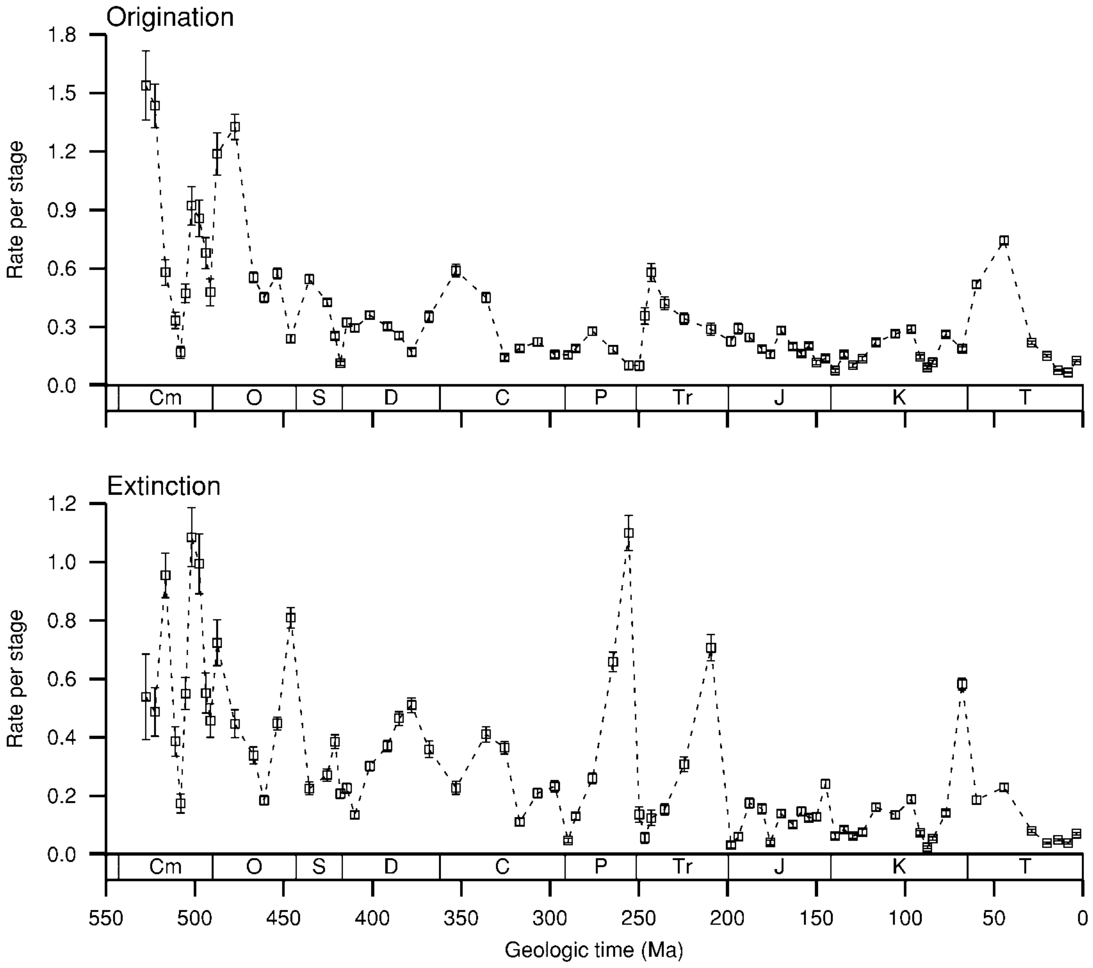

Figure 1. Observed per capita rates of origination and extinction for 31,061 genera of marine animals and animal-like protists, assuming the model of continuous turnover within intervals. These rates are based on data taken at face value, i.e., assuming first and last appearances represent origination and extinction events. Origination and extinction rates are calculated as $-\ln[X_{bt}/(X_{Ft}+X_{bt})]$ and $-\ln[X_{bt}/(X_{bL}+X_{bt})]$ (Foote 2000*a*). Error bars show ±1 SE on the basis of bootstrap resampling of genus ranges. Because of edge effects, only Tommotian through Pliocene points are plotted in this and subsequent figures.

(fig. 5). Otherwise, the two models yield preservation rates that tend to agree fairly well. Since the two sets of solutions use the same data, this may not be surprising. What is striking, however, is that the preservation rates estimated from taxonomic survivorship data also bear many similarities in temporal pattern to those calibrated from recent estimates of the amount of preserved sedimentary rock (number of marine formations; Peters and Foote 2002), shown as the dashed line in figure 5. The fair correspondence between preservation estimates that derive from completely different kinds of analysis applied to independent data of a fundamentally different nature lends further support to this approach of estimating preservation rates from first and last appearances alone. Among the most conspicuous discordances between the two sets of preservation rates, bearing in mind that the ordinate in figure 5 is logarithmic, is the fact that the sediment-based estimate is substantially lower for much of the Mesozoic and higher for the Upper Carboniferous. The first discrepancy largely reflects the fact that this particular data set on sedimentary rock is dominated by North America, which has a relatively poor Triassic and Jurassic record (Peters and Foote 2001, 2002), and the second discrepancy results in part from the large number of relatively thin formations that have been described for cyclothemic deposits (Peters and Foote 2001).

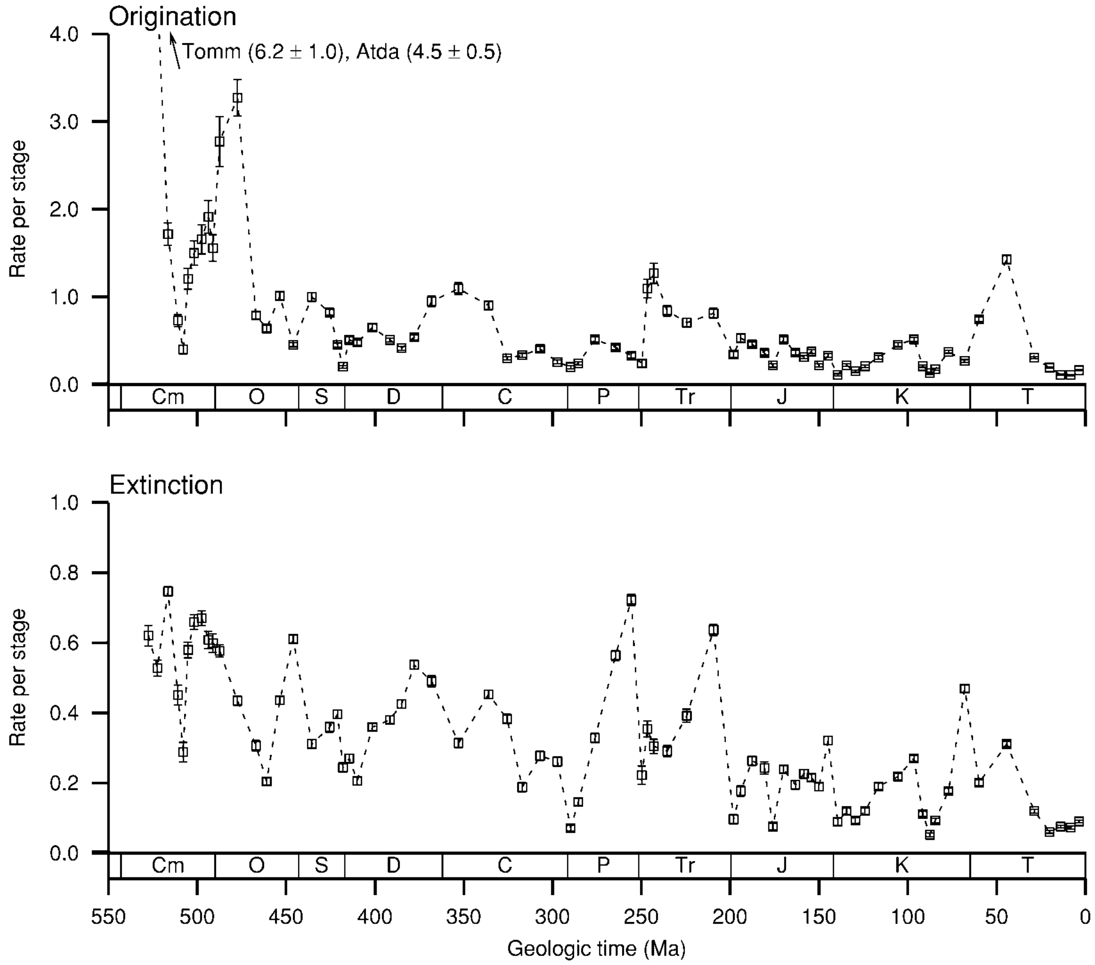

Figure 2. Observed rates of origination and extinction on the basis of the pulsed turnover model, with all originations and extinctions assumed to occur at stage beginnings and ends, respectively. Origination rate is equal to number of new genera in interval divided by number at start of interval, i.e., $(X_{FL} + X_{Ft})/(X_{bL} + X_{bt})$. Extinction rate is equal to number of genera last appearing in interval divided by total interval diversity, i.e., $(X_{FL} + X_{bL})/(X_{FL} + X_{bL} + X_{Ft} + X_{bt})$. Compare with figure 1. As with figure 1, first and last appearances are accepted as proxies for origination and extinction events.

Raw versus Revised Rates. Perhaps the most striking difference between the revised rates obtained with the continuous and pulsed models is exactly what one would expect in light of the interplay between evolutionary models and their implicit assumptions about preservation. Origination peaks often occur later in time and extinction peaks earlier with the pulsed model than with the continuous model. In addition to this expected pattern, there is also a distinct tendency for extinction peaks to coincide with peaks in the raw data (fig. 4), although there are notable exceptions such as the Late Devonian. Revised origination rates, by contrast, agree less strongly with raw values than do extinction rates.

The taxonomic rates estimated here are about 0.35 per genus per stage averaged over the Phanerozoic (in other words, mean genus duration is about three stages). Thus, the average stage length—and, by necessity, the offset between raw and revised rate peaks when these do not coincide—is on the order of about one-third the mean genus duration.

In addition to displacements relative to peaks in the raw data, the revised estimates under the continuous turnover model show a few instances in which a single peak in the raw data corresponds to

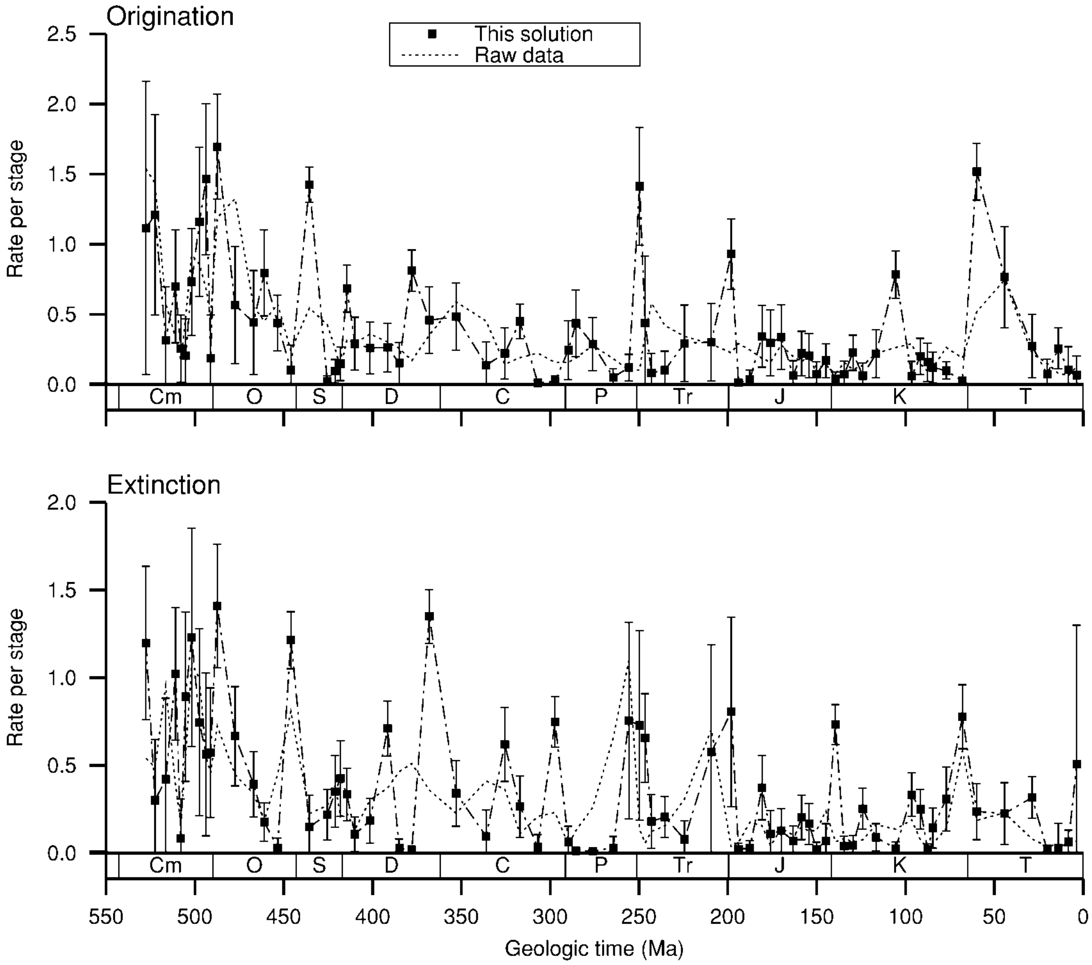

Figure 3. Revised taxonomic rates under continuous model, showing true origination and extinction rates that most closely agree with pattern of observed first and last appearances. See figure 5 for corresponding preservation rates. Error bars show ±1 SE on the basis of 100 independent estimates, each using a different bootstrap sample of the data. Dashed lines replicate apparent rates from figure 1. This solution shows many significant peaks, but these tend not to correspond in time with the apparent peaks in the raw data.

two successive intervals with above-average rates but with large error estimates on these rates. Peaks in the raw data that follow this pattern include apparent extinction in the Tatarian and Norian (fig. 3). In such cases, the existence of high rates is fairly unambiguous, but their timing is uncertain.

Closer analysis of the results yields some insight into the large uncertainty in rate estimates for these pairs of neighboring stages. Figure 6 shows, for selected pairs of stages, the rate estimates for all solutions that were combined to produce figures 3 and 4. In the first two panels, the estimates are negatively correlated. Thus, for example, a high extinction peak in the Norian can be made to fit the observed data about as well as an extinction peak in the Hettangian, but a postulated time series with anomalies in both stages would require intermediate values for these rates. A solution with a peak in neither stage would also conflict seriously with the data. A different situation holds for extinction in the Emsian and Eifelian under the pulsed model. Here high extinction-rate estimates with small uncertainties (fig. 4) imply that all viable solutions include high rates for both intervals. It is not clear why adjacent stages with elevated but highly uncertain rates are confined to the solutions involving the continuous rate model. One possibility is that turnover is truly pulsed. If most extinctions occurred at the boundaries between stages, then, under the continuous turnover model, it would be arbitrary to assign these events to one stage or the other.

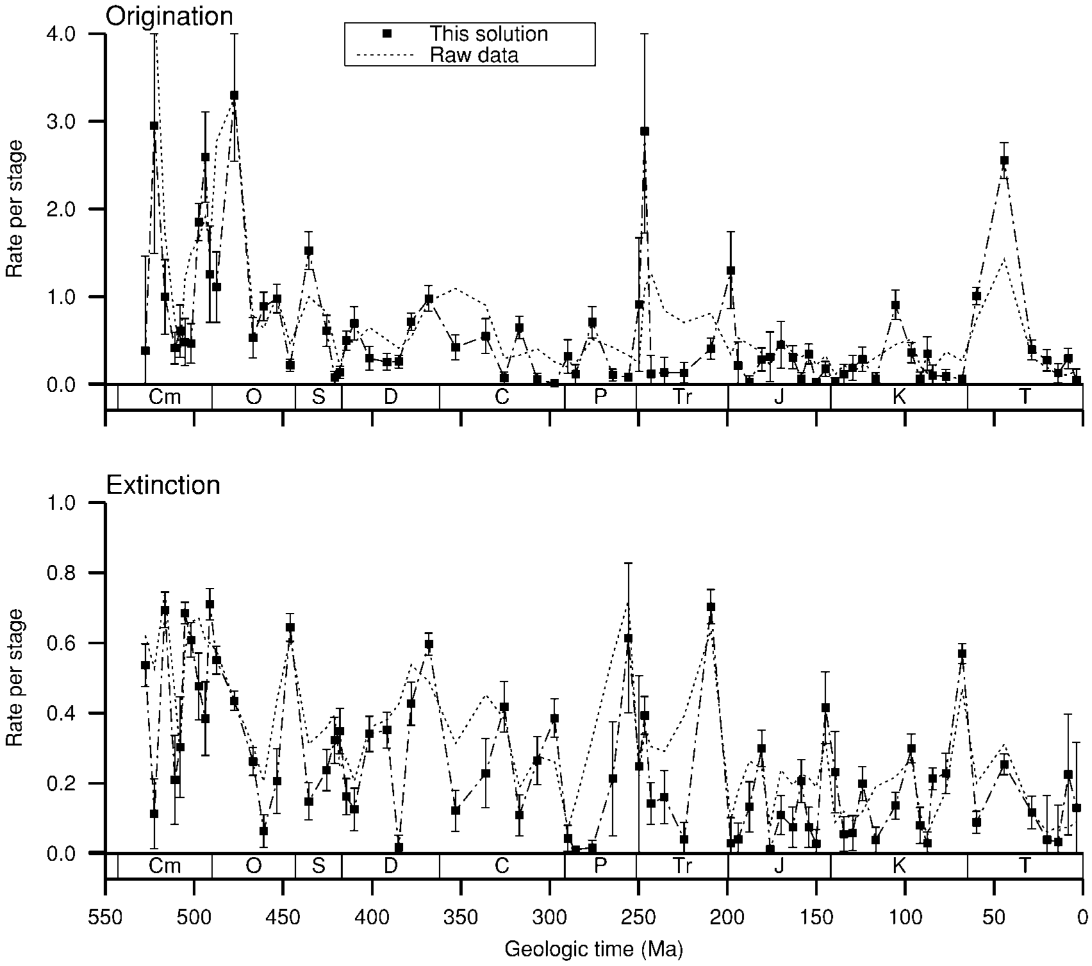

Figure 4. Revised taxonomic rates, assuming pulsed turnover model. Compare with figures 2 and 3. Dashed lines replicate apparent rates from figure 2. Extinction peaks tend to coincide with peaks in the raw data.

Constraining Preservation Rates. It should be possible to obtain more tightly constrained estimates of origination and extinction rates if accurate preservation rates can be specified (Connolly and Miller 2001*b*; Foote 2001*a*), but these estimates will tend to be biased to the extent that the specified preservation rates are incorrect. Figures 7 and 8 show taxonomic rate estimates obtained by forcing preservation rates to take on values calibrated from the amount of preserved sedimentary rock (fig. 5; Peters and Foote 2002). Just like the model of Peters and Foote (2002), these analyses assume that preservation probability per stage is equal to $1 - (1 - P)^F$, where F is the number of formations and the constant P is the probability of recovery per genus per formation. Rather than assuming a value of P, however, it was treated as a free parameter to be fitted by the optimization procedure. The values obtained, $P = 0.0123 \pm 0.00053$ for the continuous turnover model and $P = 0.0130 \pm 0.00063$ for the pulsed model, are similar to the value of $P = 0.01$ used by Peters and Foote (2002).

The taxonomic rates estimated via constrained preservation rates agree in many respects with the unconstrained estimates (figs. 7, 8). As stated above, however, the preservational constraint is far from ideal. Of course, the more complex model (with unconstrained preservation) must fit the data better than the simpler model (with constrained preservation), but is the improvement in fit sufficient to warrant the 75 additional parameters that must be estimated? A standard approach to addressing this question is to compute, for each model, Akaike's (1973) information criterion (AIC), which essentially weighs the complexity of the model against its explanatory power (Burnham and Anderson 1998; Connolly and Miller 2001*a*, 2001*b*,

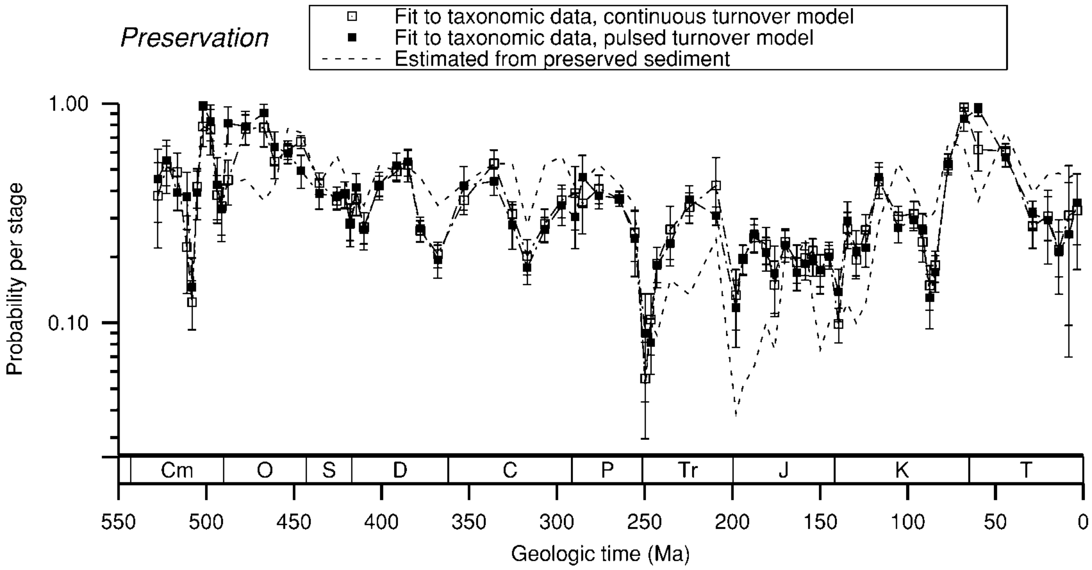

Figure 5. Estimated preservation probabilities per genus per interval. Also shown as the dashed line is an independent estimate based on a tabulation of the amount of preserved marine sedimentary rock (Peters and Foote 2002). Cambrian values are poorly constrained (Peters and Foote 2002) and are therefore omitted. Estimated rates from the two optimizations show many similarities with each other and with this independent empirical estimate. This rock-based estimate was obtained by tabulating a sample of marine sedimentary formations and assigning them to stages. If F is the number of formations in a stage and P is the assumed probability of recovery per genus per formation, then the probability of preservation per genus per stage R is equal to $1 - (1 - P)^F$. For this analysis, P was set to 0.013 (see text) and assumed constant. Because R scales monotonically to F, however, the particular value of P is not very important for the temporal pattern in R, although it does set the average level of the dashed curve. There is a nonlinear relationship between per capita preservation rate and preservation probability; if r is the rate of preservation in terms of occurrences per genus per stage, and if R is the probability that a genus ranging through an entire stage will be preserved at least once in that stage, then $R = 1 - e^{-r}$. Thus, if r is so high that R is near unity, r is free to vary over a wide range of values without affecting R. For this reason, preservation is expressed here as the probability R rather than the per capita rate r.

2002). To employ this approach, one first requires maximum-likelihood estimators of the parameters under each model. These were obtained by modifying the optimization procedure to maximize the log-likelihood or support function

$$S = \sum_{i=1}^{n}\sum_{j=i}^{n} X_{ij}\ln(P_{\rightarrow ij}) + \sum_{j=1}^{n}\sum_{i=1}^{j} X_{ij}\ln(P_{\leftarrow ij}).$$

I previously noted (Foote 2001*b*) that parameter estimates obtained by applying this approach to simulated data do not always agree with the true rates used to generate the data, whereas minimizing log deviations tends to result in accurate parameter estimates. Nevertheless, for the genus data analyzed here, the parameter estimates obtained with the two optimization criteria are in close agreement for most stages, so it is probably reasonable to use the maximum-likelihood solution to compare alternative models. For each model, the AIC is computed as $-2S + 2k$, where k is the number of parameters estimated from the data. The model with the smaller AIC value is generally preferred on information-theoretic grounds. For the continuous turnover solutions, averaged over 100 optimizations, the more complex preservational model has an AIC of 162,000 ± 910, and the model with constrained preservation rates fares worse, with an AIC of 165,000 ± 980. For the pulsed turnover solutions, the corresponding numbers are 161,000 ± 1100 and 163,000 ± 1100. The models with constrained preservation yield higher AIC values, from which we can infer that the empirical preservation constraints are generally not adequate to explain the data. This result should not be surprising in light of the deficiencies noted above, especially with respect to the data on Mesozoic sediments. Other standard information criteria that explicitly take sample size into consideration—namely, $\mathrm{AIC_c}$ and CAIC (Anderson et al. 1994)—yield similar re-

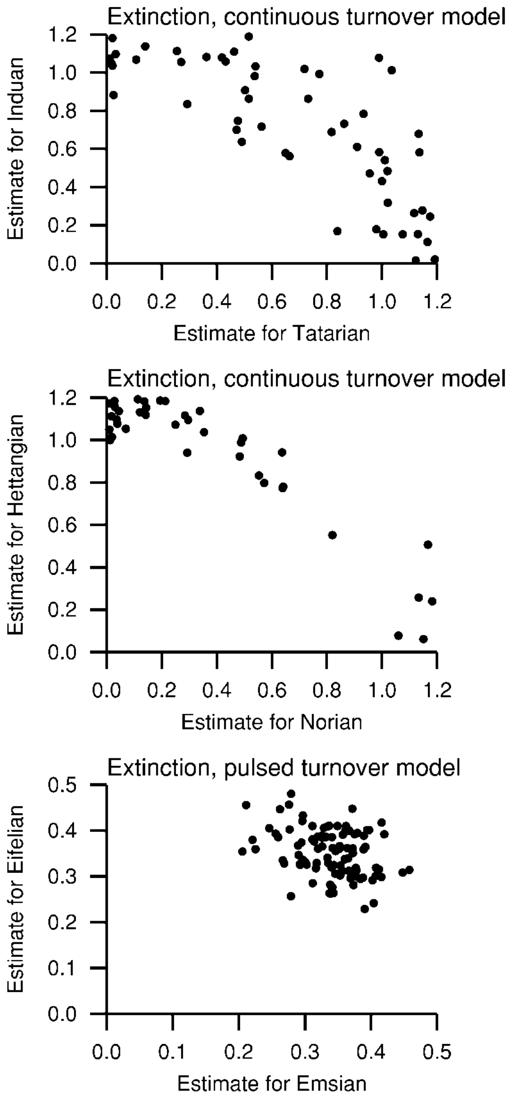

Figure 6. Revised rate estimates for selected pairs of adjacent stages. Each point shows the estimate for a single solution, of which there are 100. Cases with a strong negative correlation indicate that data are consistent with high rates in one stage or the other, but not both. These correlated rate estimates help account for some poorly resolved peaks in figure 2.

sults. If, following Peters and Foote (2002), preservation is empirically constrained and origination and extinction are constrained to be constant throughout the Phanerozoic so that only five parameters are estimated from the data, the AIC values are 177,000 ± 1000 and 176,000 ± 990 for the continuous and pulsed models. Even though the model of constant taxonomic rates can predict substantial variation in the observed extinction record (Peters and Foote 2002), the fully time-varying model is preferable according to this test.

Summary. Rate peaks appear to be real regardless of which evolutionary model is assumed and whether preservation rates are fitted to the data or constrained empirically. The inferred timing of these peaks, however, depends in many cases on whether taxonomic turnover within stages is assumed to be continuous or pulsed.

Fidelity of the Fossil Record

Considering rates for all stages rather than just the most conspicuous peaks, we can compare raw and revised rates to gain a sense of how well we would do to trust the data at face value. In order to factor out secular trends and to emphasize short-term variation, figure 9 portrays stage-to-stage changes (first differences) in rates taken from the raw data and in revised rates. Similar results (not presented) are obtained if the data are detrended by analyzing residuals of a locally weighted (LOWESS) smoothing of the rate data as a function of time. Although both the continuous and pulsed models yield rate estimates that are positively correlated with the rates tabulated from the raw data, most of these correlations are weak, and the only correspondence that inspires any confidence is that for extinction under the pulsed model. The discordance between observed and revised rates does not reflect a poor fit between model and data, since the apparent rates predicted by the solution are actually in fairly close agreement with the apparent rates observed in the fossil record (fig. 10).

Why should extinction have higher fidelity than origination, especially under the pulsed turnover model? Some insight into this question is gained if we compare revised turnover rates with inferred rates of preservation.

If we focus on the larger peaks in revised rates and on the pulsed turnover model, in which the difference in fidelity between origination and extinction is most striking and therefore most in need of explanation, we see that origination and extinction events tend to covary with preservation in different ways (figs. 4, 5). Specifically, in those cases in which an extinction excursion is followed by an elevated origination rate, there is a general tendency for preservation to decline from the extinction stage to the origination stage (table 2). Inspection of the excursions in the continuous rate solution (not presented) shows the same tendency. Because the estimated preservation rates reflect not only the quality of the fossil record but also how well it is sampled, the correlation between extinc-

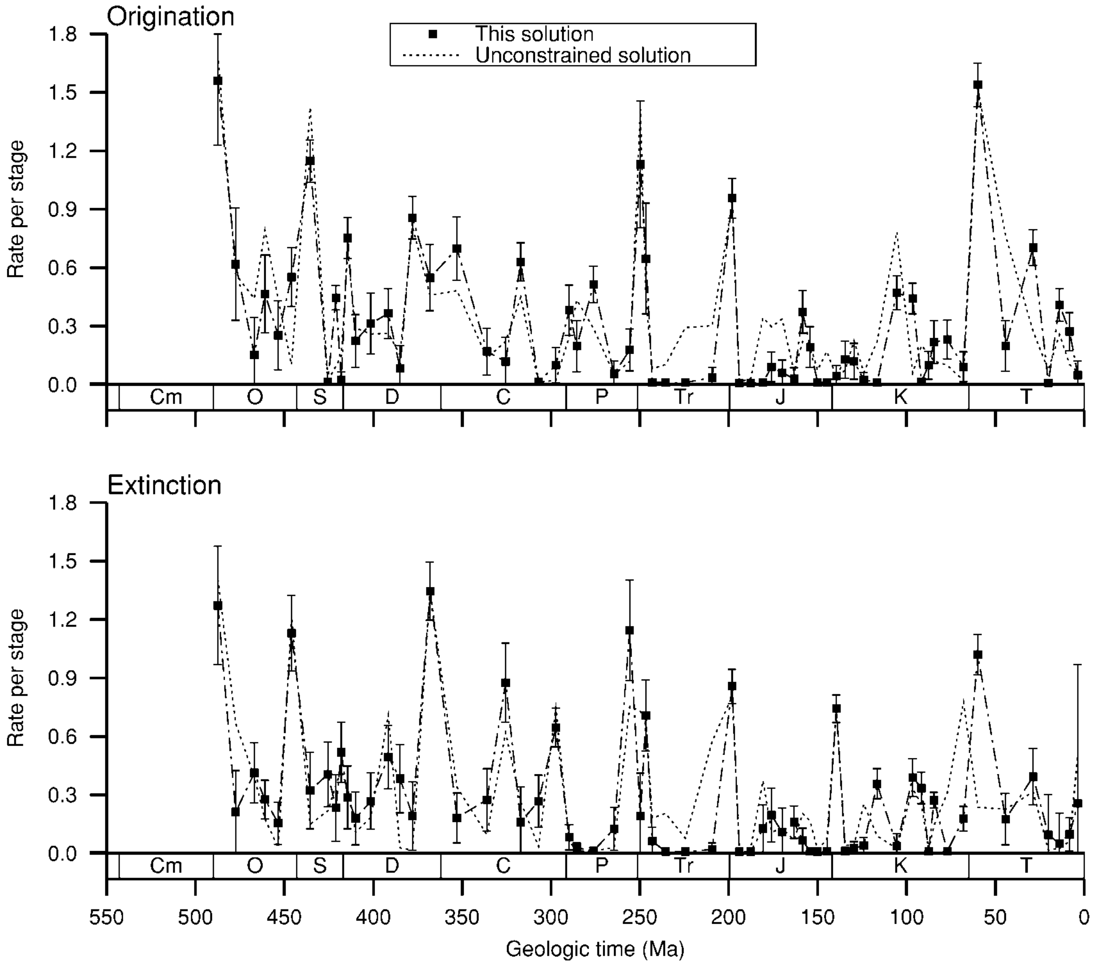

Figure 7. Revised rate estimates, assuming continuous model and constraining preservation rates to follow empirical estimate based on sedimentary rock formations (see fig. 5). Because this rock tabulation is deficient for the Cambrian (Peters and Foote 2002), only the Ordovician through Tertiary are shown. Dashed line shows unconstrained solution from figure 3. Note overall similarity between constrained and unconstrained solutions.

tion and preservation could, in principle, reflect the mere fact that intervals with known extinctions tend to be sampled intensively. This possibility is ruled out, however, by the fact that the same pattern is seen if preservation rates are calibrated empirically on the basis of the amount of preserved sedimentary rock (fig. 5; table 2).

The correspondence between apparent biotic turnover and factors such as transgression and regression, which affect the completeness of the stratigraphic record, has long been noted (Newell 1967; Holland 1995; MacLeod et al. 1997; Hallam and Wignall 1999; Smith et al. 2001; Peters and Foote 2002). Because the specter of artifact has often loomed over these discussions, it bears repeating that the results presented here do not rely on the assumption that observed first and last occurrences are good proxies for true originations and extinctions.

Discussion

I have not analyzed distinct components of the data, such as taxonomic or ecologic groups. The focus of this study has been on the modest but necessary goal of constraining the magnitude and timing of rates that stand above background, rather than the kind of geographic and biologic dissection that would permit further insight into mechanisms of mass extinction and evolutionary radiation (Miller 1997*a*, 1998; Miller and Mao 1998), or the analysis of facies relationships that may affect real or apparent patterns for particular biologic groups (e.g., Erwin 1989; Sheehan and Coorough 1990; Ja-

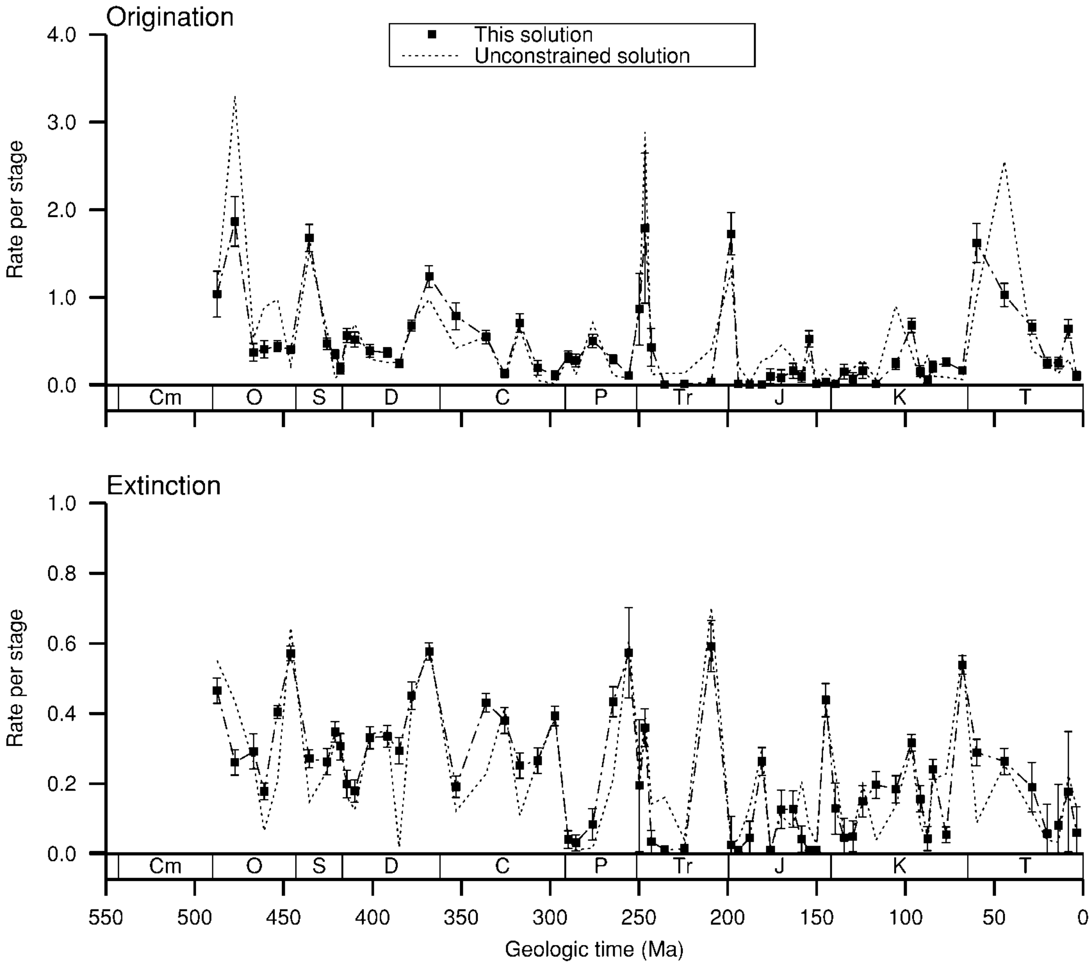

Figure 8. Revised rate estimates, assuming pulsed model and constraining preservation rates to follow empirical estimate based on sedimentary rock formations (see fig. 5). Dashed line shows unconstrained solution from figure 4. Note overall similarity between constrained and unconstrained solutions.

blonski and Raup 1995; MacLeod et al. 1997; Smith and Jeffery 1998). The reason for these limitations is largely practical. The analyses discussed herein and the sensitivity analyses needed to support them required more than 8500 h (>350 d) of CPU time on 500-Mhz Pentium III processors. Thus, repeating even a reasonable subset of these analyses for all the major taxonomic groups would at this point be prohibitive. Current developments in massively parallel computing give hope that this limitation will soon be overcome.

I have attempted to determine the true patterns of origination and extinction most consistent with observed data on first and last appearances. Of course, the results are only as reliable as the data. Limitations in global correlation will affect the quality of data, but the stratigraphic binning in this study is coarse enough that this is likely to be only a minor problem for most intervals. Nevertheless, it must be emphasized that the methods used can only account for distortion caused by incompleteness of the fossil record. They are still vulnerable to variation in taxonomic practice, such as the tendency to give different names to the same lineage on either side of a well-known turnover event (Fortey 1989; Smith 1994). To be effective, taxonomic standardization must not focus solely on the putative interval of turnover (e.g., Jeffery 2001; Smith et al. 2001) but must also encompass the longer history of a group (e.g., Culver et al. 1987; Adrain and Westrop 2000), so that the magnitude of the event can be assessed relative to background levels of turnover. Although cases of extensive pseudoorigination and pseudoextinction have been documented, for example, in latest Cambrian trilobites (Whittington 1954; Fortey 1983, 1989; Briggs et al.

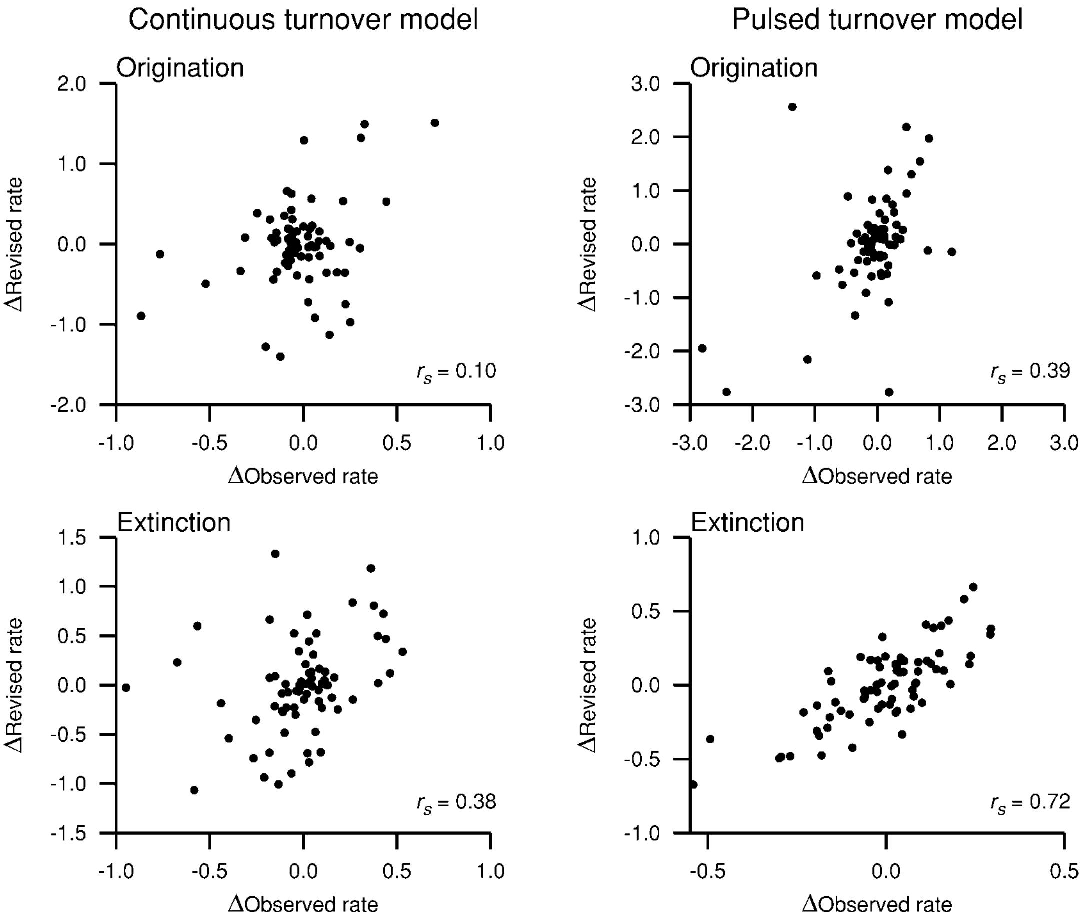

Figure 9. Comparison between observed and revised rates. To reduce effect of secular trends and to emphasize short-term variation in rates, interval-to-interval changes (first differences) are compared. Spearman rank-order correlation coefficients are given. Similar results hold for product-moment correlation coefficients.

1988; Edgecombe 1992), there are also events that are known to reflect abundant lineage origination and termination, for example, in Late Ordovician trilobites (Briggs et al. 1988; Fortey 1989). On the whole, the empirical role of taxonomic artifact in determining patterns of origination and extinction remains an important but open question.

Provided that observed peaks in first and last appearances are not attributable solely to mere name changes, the revised rate estimates suggest that these peaks reflect real origination and extinction anomalies rather than artifacts of incomplete preservation.

There is at least one additional bias, however, which could in principle imply that this conclusion is too optimistic. The approach to rate estimation assumes that the probability of sampling is effectively uniform within an interval of time. Some support for this assumption comes from the fact that different continents may share similar histories of sediment accumulation because of either eustatic sea level variation (Vail et al. 1977) or correlated cratonic uplift and subsidence (Sloss 1976). A factor that would lead one to question this assumption, however, is that outcrop is nevertheless patchily distributed geographically. If many endemic genera in reality persisted from one time interval to the next but the outcrop were in different places in successive intervals, it would appear artificially as if there were an extinction event followed by an origination event. The method used here would be tricked by this and would falsely conclude that there had been real turnover.

To what extent are observed extinction and origination events artifacts of this combination of endemism and sparse geographic sampling? A comprehensive answer is not yet available, but at least two extinction events can be identified in which

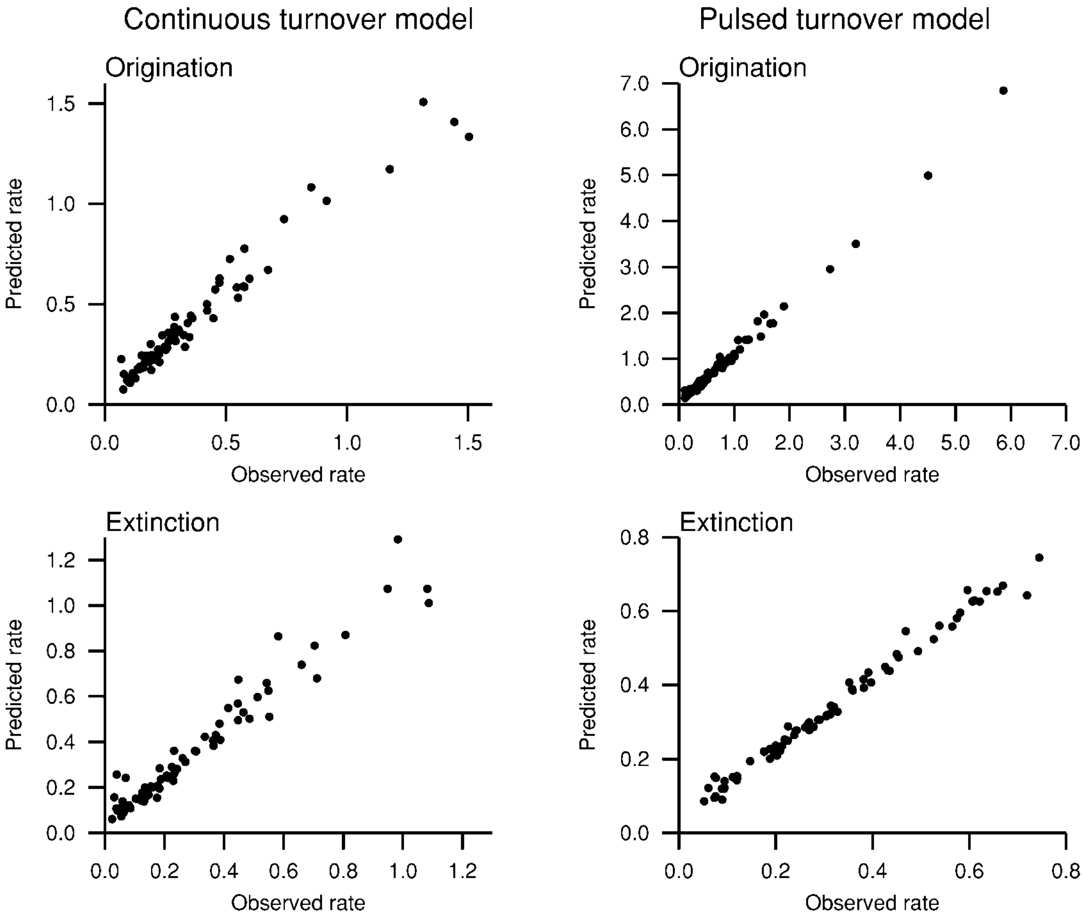

Figure 10. Comparison between observed rates and rates predicted by filtering the best-fit estimates of origination and extinction rates through the best-fit estimate of preservation rates, using equations (1)–(4). There is a close agreement between model and data.

this mechanism is probably not responsible for the large number of last appearances. Jablonski and Raup (1995; fig. 3) found that apparent extinction intensity of marine bivalve genera in the Maastrichtian declines with geographic range. This result in itself is consistent both with a biological interpretation, namely, that more widespread genera are more resistant to extinction, and with the possibility that narrowly distributed genera have artificially inflated extinction intensities because they are less likely to be sampled after the extinction event. It is difficult to argue that the extinction event is altogether an artifact, however, because the apparent extinction intensity of the widespread genera is substantially higher than the background extinction intensity for the stages leading up to the Maastrichtian (Jablonski and Raup 1995).

A new analysis of data on Ordovician marine invertebrates leads to a similar conclusion. Genus-level occurrences were downloaded from the Paleobiology Database (http://www.paleodb.org), and these were supplemented by data kindly supplied by A. I. Miller (pers. comm., 2000). For the Llanvirnian through Ashgillian, genus occurrences were assigned to paleocontinents (see Miller and Mao 1995, 1998; Miller 1997*a*, 1997*b*). Genera were then partitioned into those confined to a single paleocontinent in the given time interval, those known from two paleocontinents, and so on. The stratigraphic ranges of genera in Sepkoski's database were used to calculate apparent extinction intensity (i.e., not revised to take incompleteness into account). Figure 11 compares the percent extinction per interval with geographic range. This extinction measure was used to facilitate comparison with Jablonski and Raup's (1995) results, but similar results are obtained with the per capita extinction rate. There are two salient results in figure 11.

First, apparent extinction intensity in all time intervals is inversely correlated with geographic range. Second, and more important for this discussion, widespread Ashgillian genera have a rate of disappearance that is generally higher than the rate for geographically restricted genera earlier in the Ordovician. It is therefore hard to maintain that the high rate of extinction in the Ashgillian is an artifact of endemism coupled with geographically discontinuous sampling from the Ordovician into the Silurian.

These analyses of geographic distribution are by no means the last word on the subject, and I would not want to stifle future discussion by asserting that all sources of artifact have been ruled out. I would submit, however, that the analyses presented in this article have subjected the fossil record to a few rigorous tests and that it has passed them insofar as observed rate anomalies seem not to be explained away as artifacts. I keenly hope that others will continue to propose and test mechanisms that could cause the record to be distorted not only in a general sense but also in particular instances, especially in ways that would thwart the methods used herein. In the meantime, there is some reason to suppose that there really have been profound origination and extinction peaks throughout the Phanerozoic.

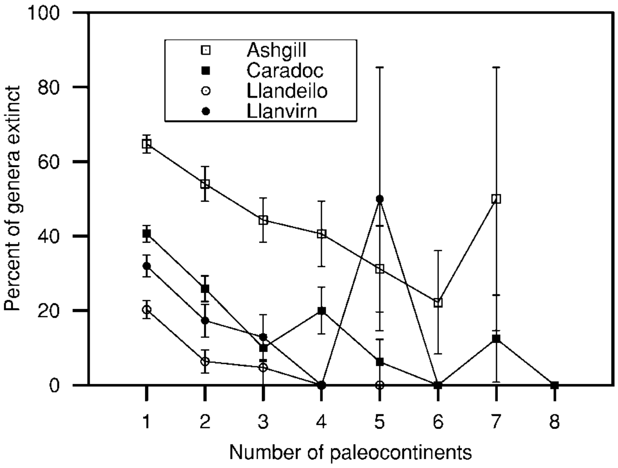

Figure 11. Relationship between geographic range and observed extinction intensity for Ordovician marine invertebrates. Error bars show ±1 SE on the basis of binomial sampling.

True rates of taxonomic turnover appear to be nonrandomly associated with the quality of the fossil record, presumably via a common latent cause (Peters and Foote 2002). The greater fidelity of extinction versus origination (figs. 1–4; table 2) suggests that the larger extinction events occur just as the record is starting to decline in quality, either shortly before or coincident with major regressions (see Hallam and Wignall 1999; Smith et al. 2001). This correlation with sea-level variation seems to hold for extinction in the Ashgillian, Tatarian, Norian, and Maastrichtian, for example (Holland and Patzkowsky 1996; de Graciansky et al. 1998, chart 1; Jacquin and de Graciansky 1998; Hallam and Wignall 1999). Biological recovery in the wake of extinction events, by contrast, occurs when the record is relatively poor, in some cases evidently because of relatively low sea level. Examples include the Llandoverian, Late Devonian, Early Triassic, and Hettangian (Hallam 1994; Ross and Ross 1996; de Graciansky et al. 1998, chart 1; Jacquin and de Graciansky 1998; Hallam and Wignall 1999). Smith et al. (2001) pointed out that there is no widely accepted, general mechanism to link sea-level variation with biotic turnover at a global scale, and they suggested that the apparent correlation be-

Table 2. Preservation Probability per Genus per Stage for Adjacent Stages

Extinction stage	Fitted rate	Empirical rate	Origination stage	Fitted rate	Empirical rate
Ashgillian	.50 ± .085	.74	Llandoverian	.39 ± .059	.43
Frasnian	.27 ± .034	.46	Famennian	.19 ± .033	.35
Serpukhovian	.28 ± .065	.54	Bashkirian	.18 ± .029	.28
Stephanian	.34 ± .065	.58	Asselian	.30 ± .086	.42
Tatarian	.24 ± .080	.35	Induan	.090 ± .046	.052
			Olenekian	.081 ± .023	.10
Norian[a]	.31 ± .030	.24	Hettangian	.12 ± .040	.039
Callovian	.19 ± .029	.24	Oxfordian	.19 ± .030	.12
Cenomanian	.30 ± .032	.41	Turonian[b]	.26 ± .051	.32
			Coniacian[b]	.13 ± .036	.30
Maastrichtian	.85 ± .10	.64	Paleocene	.95 ± .070	.36
			Eocene	.57 ± .055	.75

Note. Stages show extinction excursion followed by origination excursion, on the basis of pulsed turnover model. Shown for comparison are empirical preservation probabilities constrained by amount of preserved sedimentary rock (see fig. 5).

[a] Includes Rhaetian.

[b] Turonian immediately follows Cenomanian, but elevated origination is in Coniacian.

tween extinction and sea-level change may be more artificial than real (see also Smith 2001). Although the results presented here do not identify origination or extinction mechanisms, they do imply that the correlation is real rather than artificial in a number of cases. The precise nature of the joint controls on evolution and stratigraphy clearly deserves further attention (Holland 1995; Patzkowsky and Holland 1996).

In light of the revised rate estimates obtained under the continuous versus pulsed models, it is evident that assessing the fidelity of the fossil record of origination and extinction is largely, albeit not entirely, a matter of determining whether true taxonomic rates within stages are closer to one model or the other. If originations and extinctions are spread throughout stages, then observed first and last appearances at the stage level are misleading and a number of true rate peaks are likely to have occurred one stage before or after that in which they appear in the raw data. If rates are highly pulsed, by contrast, with turnover concentrated at stage boundaries, then a fair number of extinction peaks—but to a much lesser extent origination peaks—may be faithful essentially at face value.

Abundant, among-stage variation in turnover rates (Raup 1991) is equally consistent with continuous or pulsed variation within the stage. Determining whether the pulsed or smooth model of rate variation is more appropriate will therefore ultimately require data on taxonomic occurrences at a much finer scale of stratigraphic resolution than that which is used here (e.g., Hallam 1986; Jablonski 1986; Kauffman and Harries 1996; Smith et al. 2001; House 2002). The biostratigraphic literature is replete with high-resolution data on taxonomic occurrences. It is therefore reasonable to suppose that addressing the question of continuous versus pulsed turnover may be more a matter of compiling existing data at a large scale (Alroy et al. 2001) and analyzing them appropriately rather than collecting new data. Of course, raw patterns of first and last appearance in fine-scale stratigraphic occurrence data, especially if biased by factors that particularly affect single sections or regions (Holland 1995), will not by themselves answer the question of continuous versus pulsed turnover. Such patterns must be analyzed in a way that takes incompleteness into consideration (Kemple et al. 1995; Cooper et al. 2001). Unfortunately, this has generally not been done. I would offer a few general observations and recommendations.

1. One important approach to testing whether clusters of first and last appearances provide support for the pulsed turnover model is to determine whether they occur at times when they would not be predicted as artifacts, for example, within highstands as opposed to flooding surfaces or sequence boundaries. Holland (1995) applied this strategy to Upper Ordovician sections in the Cincinnati Arch to distinguish those turnover pulses that are likely to be real from those that may be artificial. Smith et al. (2001) also studied last appearances in a sequence-stratigraphic context, arguing that an apparent extinction excursion in the Cenomanian occurs precisely where one would expect it as an artifact.

2. Confidence limits on stratigraphic ranges represent another approach with which to assess turnover models. For example, on the basis of occurrences leading up to the Cretaceous/Tertiary boundary at Zumaya, Spain, and related localities, Marshall and Ward (1996) found that true extinctions for a subset of Maastrichtian ammonoids were likely to be clustered. A similar analysis by Raup (1989) suggested a mixture of gradual extinction leading up to the K/T boundary and a final pulse at the boundary. Because these analyses assume uniform preservation not only throughout the Maastrichtian but also into the Paleocene, the survival of lineages into the Tertiary cannot be ruled out if there is in reality a change in preservation potential around the K/T (MacLeod et al. 1997). Nevertheless, the hypothesis of a constant, elevated extinction rate throughout the late Maastrichtian is not supported. Similar analyses argue against gradual extinction in the Late Permian (Jin et al. 2000). To be maximally useful, calculation of confidence limits to determine whether true turnover is pulsed should avoid the assumption of uniform preservation probability. This step has not generally been taken, but it can be effected, for example, by constraining preservation on the basis of knowledge of sequence stratigraphy or density of sampling (Marshall 1997; Connolly and Miller 2001*a*).

3. As discussed above, the pattern of extinction in the stage following the cluster of last appearances (and that of origination in the stage preceding a cluster of first appearances) must be constrained in addition to the pattern in the stage of apparent turnover. To determine whether there was a true extinction peak in the Tatarian, for example, we need to know not only whether extinction follows the pulsed model in the Late Permian but also whether it does so in the Early Triassic. This requirement has been all but overlooked in origination and extinction studies.

4. Fine-scale analysis of first appearances de-

serves the same attention that has been paid to last appearances. With a few exceptions (Holland 1995; Kemple et al. 1995; Cooper et al. 2001), the extent to which origination is pulsed in reality, not just as it appears from first appearances, has been largely ignored.

Some insight into continuous versus pulsed models should, in principle, be gained by using the methods of this article to analyze data at the substage level of resolution. The pulsed model predicts that peaks evident at the stage level should tend to be resolved as single peaks at the substage level. Unfortunately, the data are sparse at this level. Only about 60% of the genera resolved to the stage level are also resolved to the substage level, and the substantially smaller number of first and last appearances is spread out over about twice the number of intervals.

Substage-level data were analyzed with a focus on the stages that flank five system boundaries with unusually high turnover (Ordovician/Silurian, Devonian/Carboniferous, Permian/Triassic, Triassic/Jurassic, and Cretaceous/Tertiary). The results (not presented here) are not entirely conclusive. Some events evident at the stage level are nearly confined to single substages, for example, extinction in the upper Ashgillian, upper Norian, and upper Maastrichtian. Others may reflect elevated rates in more than one substage. For example, under the pulsed model there is a single origination peak in the middle Llandoverian, while the continuous model yields subequal peaks in the lower and upper Llandoverian, and the continuous model yields a single Famennian peak in the upper part of this stage, while the pulsed model yields subequal rates in the middle and upper parts.

As time intervals become shorter, the continuous and pulsed models should, in principle, agree more closely, because more taxa will span the entire interval and because the difference between the models in the relevant quantities that dictate apparent survivorship (table 1) decreases as the rate per interval decreases. Substage-level rate estimates do indeed allow some discrepancies between the two models to be resolved. For example, at the stage level, the continuous model yields high origination estimates in the Induan and Paleocene, whereas the pulsed model yields peaks in the Olenekian and Eocene. At the substage level, both models yield peaks in the lower Olenekian, the lower Paleocene, and the lower Eocene.

For a wide range of questions, it is the reality of rate peaks rather than their exact placement that matters. Examples include the nature of selectivity and whether extinction events disrupt long-term evolutionary trends (Jablonski 1991, 1998; Hallam and Wignall 1997). For other questions, however, the timing of events is crucial. These include the statistical lag between origination and extinction (Hallam 1991; Erwin 1998; Kirchner and Weil 2000*b*) and the relationship between short-term diversity fluctuations and variation in taxonomic rates (Foote 2000*b*). The face-value timing of origination and extinction peaks seems in some cases to be clearly reliable and in others to be clearly unreliable. For example, the origination peak in the Llandoverian and the extinction peaks in the Ashgillian and Maastrichtian are present in both the raw data and the revised rate estimates regardless of the evolutionary model assumed, and the continuous and pulsed models agree in pushing the apparent origination peak of the Anisian back into the Induan or Olenekian. In many cases, however, the continuous and pulsed models yield discordant results, and deciding when an event occurred therefore requires additional information on temporal variation in taxonomic rates at a finer scale than is generally available in global databases such as the one analyzed here.

Conclusions

1. Reanalysis of stratigraphic range data for Phanerozoic marine genera enables the reality and timing of origination and extinction events to be assessed critically.

2. The timing of a few apparent events is demonstrably reliable or unreliable. The timing of many, however, is ambiguous.

3. Despite uncertainties in the timing of rate peaks seen in the raw data, the reality of such peaks is largely supported by the analyses presented here. Thus, studies that rely only on the existence of rate anomalies, irrespective of their precise magnitude and timing, are generally upheld. Previous work has shown an agreement between the observed extinction record and what one would expect from a constant extinction rate distorted on the basis of known variability in the fossil record. This agreement is likely to reflect a common latent cause that affects true extinction and the quality of the fossil record.

4. There is some indication that the record of origination is more seriously distorted by incomplete and variable preservation than is that of extinction. Extinction events have a somewhat greater tendency to occur during stages with high preservation potential, while origination events that follow these extinctions are more likely to occur during times that are more poorly represented.

These factors may tend to exaggerate artificially the lag between extinction and origination events. More generally, studies that have interpreted the covariation between raw origination and extinction rates may need to be reconsidered.

5. Certain distorting factors, such as taxonomic practice and geographic and environmental heterogeneity of sampling, are likely still to affect perceived patterns of origination and extinction. That these factors are at work is without question. How important they are empirically is yet to be determined.

6. Somewhat better constraints on the magnitude and timing of events may be possible with the help of independent data on preservation rates. Given the similarity among solutions that allow preservation to be fit to the taxonomic data and those that force preservation to follow empirical patterns of preserved sediment, however, it is not clear that constraining preservation will prove the ultimate key to taxonomic-rate estimation for marine animals over the course of the Phanerozoic.

7. On the basis of the results presented here, an essential component of better rate estimation will be independent evidence for the evolutionary model used to fit rates, specifically whether originations and extinctions tend to occur continuously throughout stages or to be concentrated near stage boundaries.

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REFERENCES CITED

Adrain, J. M., and Westrop, S. R. 2000. An empirical assessment of taxic paleobiology. Science 289:110–112.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. *In* Petrov, B. N., and Csáki, F., eds. 2d International Symposium on Information Theory. Budapest, Akadémiai Kiadó, p. 267–281.

Alroy, J. 1996. Constant extinction, constrained diversification, and uncoordinated stasis in North American mammals. Palaeogeogr. Palaeoclimatol. Palaeoecol. 127:285–311.

———. 1998. Equilibrial diversity dynamics in North American mammals. *In* McKinney, M. L., and Drake, J. A., eds. Biodiversity dynamics: turnover of populations, taxa, and communities. New York, Columbia University Press, p. 233–287.

Alroy, J.; Marshall, C. R.; Bambach, R. K.; Bezusko, K.; Foote, M.; Fürsich, F. T.; Hansen, T. A.; et al. 2001. Effects of sampling standardization on estimates of Phanerozoic marine diversification. Proc. Natl. Acad. Sci. USA 98:6261–6266.

Anderson, D. R.; Burnham, K. P.; and White, G. C. 1994. AIC model selection in overdispersed capture-recapture data. Ecology 75:1780–1793.

Bowring, S. A., and Erwin, D. H. 1998. A new look at evolutionary rates in deep time: uniting paleontology and high-precision geochronology. GSA Today 8:1–8.

Bowring, S. A.; Erwin, D. H.; Jin, Y. G.; Martin, M. W.; Davidek, D.; and Wang. W. 1998. U/Pb zircon geochronology and tempo of the end-Permian mass extinction. Science 280:1039–1043.

Briggs, D. E. G.; Fortey, R. A.; and Clarkson, E. N. K. 1988. Extinction and the fossil record of the arthropods. *In* Larwood, G. P., ed. Extinction and survival in the fossil record (Syst. Assoc. Spec. vol. 24). London, Academic Press, p. 171–209.

Brownie, C.; Anderson, D. R.; Burnham, K. P.; and Robson, D. S. 1985. Statistical inference from band recovery data: a handbook. 2d ed. Washington, D.C., U.S. Fish Wildl. Serv. Resour. Publ. 156, 305 p.

Burnham, K. P.; and Anderson, D. R. 1998. Model selection and inference: a practical information-theoretic approach. New York, Springer, 353 p.

Burnham, K. P.; Anderson, D. R.; White, C. G.; Brownie, C.; and Pollock, K. H. 1987. Design and analysis methods for fish survival experiments based on release-recapture. Bethesda, Md., Am. Fish. Soc. Monogr. 5, 437 p.

Connolly, S. R., and Miller, A. I. 2001*a*. Global Ordovician faunal transitions in the marine benthos: proximate causes. Paleobiology 27:779–795.

———. 2001*b*. Joint estimation of sampling and turnover rates from fossil databases: capture-mark-recapture methods revisited. Paleobiology 27:751–767.

———. 2002. Global Ordovician faunal transitions in the marine benthos: ultimate causes. Paleobiology 28: 26–40.

Conroy, M. J., and Nichols, J. D. 1984. Testing for variation in taxonomic extinction probabilities: a suggested methodology and some results. Paleobiology 10:328–337.

Cooper, R. A.; Crampton, J. S.; Raine, J. I.; Gradstein, F. M.; Morgans, H. E. G.; Sadler, P. M.; Strong, C. P.; Waghorn, D.; and Wilson, G. J. 2001. Quantitative biostratigraphy of the Taranaki Basin, New Zealand: a deterministic and probabilistic approach. AAPG Bull. 85:1469–1498.

Culver, S. J.; Buzas, M. A.; and Collins, L. S. 1987. On the value of taxonomic standardization in evolutionary studies. Paleobiology 13:169–176.

Darwin, C. E. [1859] 1964. On the origin of species by means of natural selection. London, J. Murray, 490 p. Reprint, Cambridge, Mass., Harvard University Press.

de Graciansky, P.-C.; Hardenbol, J.; Jacquin, T.; and Vail, P. R. 1998. Mesozoic and Cenozoic sequence stratigraphy of European basins. Tulsa, Okla., SEPM Spec. Publ. 60, 786 p.

Droser, M. L.; Bottjer, D. J.; Sheehan, P. M.; and McGhee, G. R., Jr. 2000. Decoupling of taxonomic and ecological severity of Phanerozoic marine mass extinctions. Geology 28:675–678.

Edgecombe, G. D. 1992. Trilobite phylogeny and the Cambrian-Ordovician "event": cladistic reappraisal. *In* Novacek, M. J., and Wheeler, Q. D., eds. Extinction and phylogeny. New York, Columbia University Press, p. 144–177.

Erwin, D. H. 1989. Regional paleoecology of Permian gastropod genera, southwestern United States and the end-Permian mass extinction. Palaios 4:424–438.

———. 1998. The end and the beginning: recoveries from mass extinctions. Trends Ecol. Evol. 13:344–349.

Foote, M. 1994. Temporal variation in extinction risk and temporal scaling of extinction metrics. Paleobiology 20:424–444.

———. 2000*a*. Origination and extinction components of taxonomic diversity: general problems. *In* Erwin, D. H., and Wing, S. L., eds. Deep time: *Paleobiology*'s perspective. Paleobiology 26(suppl.):74–102.

———. 2000*b*. Origination and extinction components of taxonomic diversity: Paleozoic and post-Paleozoic dynamics. Paleobiology 26:578–605.

———. 2001*a*. Evolutionary rates and the age distributions of living and extinct taxa. *In* Jackson, J. B. C.; McKinney, F. K.; and Lidgard, S., eds. Evolutionary patterns: growth, form, and tempo in the fossil record. Chicago, University of Chicago Press, p. 245–294.

———. 2001*b*. Inferring temporal patterns of preservation, origination, and extinction from taxonomic survivorship analysis. Paleobiology 27:602–630.

Fortey, R. A. 1983. Cambrian-Ordovician trilobites from the boundary beds in western Newfoundland and their phylogenetic significance. Spec. Pap. Palaeontol. 30: 179–211.

———. 1989. There are extinctions and extinctions: examples from the Lower Palaeozoic. Philos. Trans. R. Soc. Lond. B Biol. Sci. 325:327–355.

Gilinsky, N. L., and Bambach, R. K. 1987. Asymmetrical patterns of origination and extinction in higher taxa. Paleobiology 13:427–445.

Golonka, J., and Kiessling, W. 2002. Phanerozoic time scale and definition of time slices. *In* Kiessling, W.; Flügel, E.; and Golonka, J., eds. Phanerozoic reef patterns. Tulsa, Okla., SEPM Spec. Publ. 72, p. 11–20.

Hallam, A. 1986. The Pliensbachian and Tithonian extinction events. Nature 319:765–768.

———. 1991. Why was there a delayed radiation after the end-Paleozoic extinctions? Hist. Biol. 5:257–262.

———. 1994. Phanerozoic sea level changes. New York, Columbia University Press, 266 p.

Hallam, A., and Wignall, P. B. 1997. Mass extinctions and their aftermath. Oxford, Oxford University Press, 320 p.

———. 1999. Mass extinctions and sea-level changes. Earth Sci. Rev. 48:217–250.

Holland, S. M. 1995. The stratigraphic distribution of fossils. Paleobiology 21:92–109.

———. 2000. The quality of the fossil record: a sequence-stratigraphic perspective. *In* Erwin, D. H., and Wing, S. L., eds. Deep time: *Paleobiology*'s perspective. Paleobiology 26(suppl.):148–168.

Holland, S. M., and Patzkowsky, M. E. 1996. Sequence stratigraphy and long-term paleoceanographic change in the Middle and Upper Ordovician of the eastern United States. *In* Witzke, B. J.; Ludvigson, G. A.; and Day, J., eds. Paleozoic sequence stratigraphy: views from the North American Craton. Boulder, Colo., Geol. Soc. Am. Spec. Pap. 306, p. 117–129.

———. 2002. Stratigraphic variation in the timing of first and last occurrences. Palaios 17:134–146.

House, M. R. 2002. Strength, timing, setting and cause of mid-Palaeozoic extinctions. Palaeogeogr. Palaeoclimatol. Palaeoecol. 181:5–25.

Jablonski, D. 1986. Background and mass extinctions: the alternation of macroevolutionary regimes. Science 231:129–133.

———. 1991. Extinctions: a paleontological perspective. Science 253:754–757.

———. 1998. Geographic variation in the molluscan recovery from the end-Cretaceous extinction. Science 279:1327–1330.

Jablonski, D., and Raup, D. M. 1995. Selectivity of end-Cretaceous marine bivalve extinctions. Science 268: 389–391.

Jacquin, T., and de Graciansky, P.-C. 1998. Major transgressive/regressive cycles: the stratigraphic signature of European basin development. *In* de Graciansky, P.-C., Hardenbol, J.; Jacquin, T.; and Vail, P. R. 1998. Mesozoic and Cenozoic sequence stratigraphy of European basins. Tulsa, Okla., SEPM Spec. Publ., 60, p. 15–29.

Jeffery, C. H. 2001. Heart urchins at the Cretaceous/Tertiary boundary: a tale of two clades. Paleobiology 27: 140–158.

Jin, Y. G.; Wang, Y.; Wang, W.; Shang, Q. H.; Cao, C. Q.; and Erwin, D. H. 2000. Pattern of marine mass extinction near the Permian-Triassic boundary in South China. Science 289:432–436.

Kauffman, E. G., and Harries, P. J. 1996. The importance of crisis progenitors in recovery from mass extinction. *In* Hart, M. B., ed. Biotic recoveries from mass extinction events. London, Geol. Soc. Spec. Publ. 102, p. 15–39.

Kemple, W. G.; Sadler, P. M.; and Strauss, D. J. 1995.

Extending graphic correlation to many dimensions: stratigraphic correlation as constrained optimization. *In* Mann, K. O.; and Lane, H. R., eds. Graphic correlation. Tulsa, Okla., SEPM Spec. Publ. 53, p. 65–82.

Kendall, D. G. 1948. On the generalized "birth-and-death" process. Ann. Math. Stat. 19:1–15.

Kirchner, J. W. 2002. Evolutionary speed limits inferred from the fossil record. Nature 415:65–68.

Kirchner, J. W., and Weil, A. 2000*a*. Correlations in fossil extinction and origination rates through geological time. Proc. Biol. Sci. 267:1301–1309.

———. 2000*b*. Delayed biological recovery from extinctions throughout the fossil record. Nature 404: 177–180.

Koch, C. F. 1991. Species extinctions across the Cretaceous-Tertiary boundary: observed patterns versus predicted sampling effects, stepwise or otherwise? Hist. Biol. 5:355–361.

MacLeod, N., and Keller, G. 1991. Hiatus distributions and mass extinctions at the Cretaceous/Tertiary boundary. Geology 19:497–501.

MacLeod, N.; Rawson, P. F.; Forey, P. L.; Banner, F. T.; Boudagher-Fadel, M. K.; Bown, P. R.; Burnett, J. A.; et al. 1997. The Cretaceous-Tertiary biotic transition. J. Geol. Soc. Lond. 154:265–292.

Marshall, C. R. 1997. Confidence intervals on stratigraphic ranges with nonrandom distributions of fossil horizons. Paleobiology 23:165–173.

Marshall, C. R., and Ward, P. D. 1996. Sudden and gradual molluscan extinctions in the latest Cretaceous of western European Tethys. Science 274:1360–1363.

Metcalfe, I.; Nicoll, R. S.; Mundil, R.; Foster, C.; Glen, J.; Lyons, J.; Wang, X. F.; et al. 2001. The Permian-Triassic boundary and mass extinction in China. Episodes 24:239–244.

Miller, A. I. 1997*a*. Dissecting global diversity patterns: examples from the Ordovician Radiation. Annu. Rev. Ecol. Syst. 28:85–104.

———. 1997*b*. A new look at age and area: the geographic and environmental expansion of genera during the Ordovician Radiation. Paleobiology 23:410–419.

———. 1998. Biotic transitions in global marine diversity. Science 281:1157–1160.

Miller, A. I., and Mao, S. G. 1995. Association of orogenic activity with the Ordovician Radiation of marine life. Geology 23:305–308.

———. 1998. Scales of diversification and the Ordovician Radiation. *In* McKinney, M. L., and Drake, J. A., eds. Biodiversity dynamics: turnover of populations, taxa, and communities. New York, Columbia University Press, p. 288–310.

Mundil, R.; Metcalfe, I.; Ludwig, K. R.; Renne, P. R.; Oberli, F.; and Nicoll, R. S. 2001. Timing of the Permian-Triassic biotic crisis: implications from new zircon U/Pb age data (and their implications). Earth Planet. Sci. Lett. 187:131–145.

Newell, N. D. 1967. Revolutions in the history of life. Geol. Soc. Am. Spec. Pap. 89:63–91.

Nichols, J. D.; Hines, J. E.; Lebreton, J.-D.; and Pradel, R. 2000. Estimation of contributions to population growth: a reverse-time capture-recapture approach. Ecology 81:3362–3376.

Nichols, J. D.; Morris, R. W.; Brownie, C.; and Pollock, K. H. 1986. Sources of variation in extinction rates, turnover, and diversity of marine invertebrate families during the Paleozoic. Paleobiology 12:421–432.

Nichols, J. D., and Pollock, K. H. 1983. Estimating taxonomic diversity, extinction rates, and speciation rates from fossil data using capture-recapture models. Paleobiology 9:150–163.

Niklas, K. J., and Tiffney, B. H. 1994. The quantification of plant biodiversity through time. Philos. Trans. R. Soc. Lond. B Biol. Sci. 345:35–44.

Patzkowsky, M. E., and Holland, S. M. 1996. Extinction, invasion, and sequence stratigraphy: patterns of faunal change in the Middle and Upper Ordovician of the eastern United States. *In* Witzke, B. J.; Ludvigson, G. A.; and Day, J., eds. Paleozoic sequence stratigraphy: views from the North American Craton. Boulder, Colo., Geol. Soc. Am. Spec. Pap. 306, p. 131–142.

Peters, S. E., and Foote, M. 2001. Biodiversity in the Phanerozoic: a reinterpretation. Paleobiology 27:583–601.

———. 2002. Determinants of extinction in the fossil record. Nature 416:420–424.

Plotnick, R. E., and Sepkoski, J. J., Jr. 2001. A multiplicative multifractal model of originations and extinctions. Paleobiology 27:126–139.

Pollock, K. H.; Nichols, J. D.; Brownie, C.; and Hines, J. E. 1990. Statistical inference for capture-recapture experiments. Wildl. Monogr. 107:1–97.

Pradel, R. 1996. Utilization of capture-mark-recapture for the study of recruitment and population growth rate. Biometrics 52:703–709.

Press, W. H.; Teukolsky, S. A.; Vetterling, W. T.; and Flannery, B. P. 1992. Numerical recipes in C. 2d ed. Cambridge, Cambridge University Press, 994 p.

Raup, D. M. 1978. Cohort analysis of generic survivorship. Paleobiology 4:1–15.

———. 1989. The case for extraterrestrial causes of extinction. Philos. Trans. R. Soc. Lond. B Biol. Sci. 325: 421–431.

———. 1991. A kill curve for Phanerozoic marine species. Paleobiology 17:37–48.

Raup, D. M., and Sepkoski, J. J., Jr. 1982. Mass extinctions in the marine fossil record. Science 215:1501–1503.

Ross, C. A., and Ross, J. M. 1996. Silurian sea-level fluctuations. *In* Witzke, B. J.; Ludvigson, G. A.; and Day, J., eds. Paleozoic sequence stratigraphy: views from the North American Craton. Boulder, Colo., Geol. Soc. Am. Spec. Pap. 306, p. 187–192.

Sepkoski, J. J., Jr. 1981. A factor analytic description of the Phanerozoic marine fossil record. Paleobiology 7: 36–53.

———. 1984. A kinetic model of Phanerozoic taxonomic diversity. III. Post-Paleozoic families and mass extinctions. Paleobiology 10:246–267.

———. 1986. Phanerozoic overview of mass extinction. *In* Raup, D. M., and Jablonski, D., eds. Patterns and processes in the history of life. Berlin, Springer, p. 277–297.

———. 1992. A compendium of fossil marine animal familes. 2d ed. Milw. Public Mus. Contrib. Biol. Geol. 83:1–156.

———. 1996. Patterns of Phanerozoic extinctions: a perspective from global databases. *In* Walliser, O. H., ed. Global events and event stratigraphy. Berlin, Springer, p. 35–52.

———. 1997. Biodiversity: past, present, and future. J. Paleontol. 71:533–539.

———. 1998. Rates of speciation in the fossil record. Philos. Trans. R. Soc. Lond. B Biol. Sci 353:315–326.

———. 2002. A compendium of fossil marine animal genera. Bull. Am. Paleontol. 363:1–560.

Sheehan, P. M., and Coorough, P. J. 1990. Brachiopod zoogeography across the Ordovician-Silurian extinction event. *In* McKerrow, W. S., and Scotese, C. R., eds. Palaeozoic palaeogeography and biogeography. London, Geol. Soc. Mem. 12, p. 181–187.

Signor, P. W., III, and Lipps, J. H. 1982. Sampling bias, gradual extinction patterns and catastrophes in the fossil record. Geol. Soc. Am. Spec. Pap. 190:291–296.

Sloss, L. L. 1976. Areas and volumes of cratonic sediments, western North America and eastern Europe. Geology 4:272–276.

Smith, A. B. 1994. Systematics and the fossil record: documenting evolutionary patterns. London, Blackwell Scientific, 223 p.

———. 2001. Large-scale heterogeneity of the fossil record: implications for Phanerozoic biodiversity studies. Philos. Trans. R. Soc. Lond. B Biol. Sci. 356:1–17.

Smith, A. B.; Gale, A. S.; and Monks, N. E. A. 2001. Sea-level change and rock-record bias in the Cretaceous: a problem for extinction and biodiversity studies. Paleobiology 27:241–253.

Smith, A. B., and Jeffery, C. H. 1998. Selectiviy of extinction among sea urchins at the end of the Cretaceous period. Nature 392:69–71.

Stanley, S. M. 1990. Delayed recovery and the spacing of major extinctions. Paleobiology 16:401–414.

Vail, P. R.; Mitchum, R. M.; and Thompson, S., III. 1977. Seismic stratigraphy and global changes of sea level. 4. Global cycles of relative changes of sea level. *In* Payton, C. E., ed. Seismic stratigraphy: applications to hydrocarbon exploration. Tulsa, Okla., AAPG Mem. 26, p. 83–97.

Van Valen, L. M. 1984. A resetting of Phanerozoic community evolution. Nature 307:50–52.

———. 1994. Concepts and the nature of selection by extinction: is generalization possible? *In* Glen, W., ed. The mass extinction debates: how science works in a crisis. Stanford, Calif., Stanford University Press, p. 200–216.

Whittington, H. B. 1954. Status of invertebrate paleontology, 1953. VI. Arthropoda: Trilobita. Bull. Mus. Comp. Zool., Harvard Coll. 112:193–200.

ERRATUM

In "Origination and extinction through the Phanerozoic: a new approach" by Michael Foote (*Journal of Geology* 111:125–148), table 1 contained several errors. The corrected version of the table appears here.

Table 1. Expressions Used to Calculate Survivorship Probabilities

Quantity/model	Expression
N_{bt}:	
•C	$N_{\mathrm{b}}e^{-q}$
•P	$N_{\mathrm{b}}(1-q)$
N_{bL}:	
•C	$N_{\mathrm{b}}(1-e^{-q})$
•P	$N_{\mathrm{b}}q$
N_{Ft}:	
CC	$N_{\mathrm{b}}e^{p-q}(1-e^{-p})$
PP	$N_{\mathrm{b}}p(1-q)$
CP	$N_{\mathrm{b}}e^{p}(1-q)(1-e^{-p})$
PC	$N_{\mathrm{b}}pe^{-q}$
N_{FL}:	
CC[a]	$N_{\mathrm{b}}(e^{-q}+p-1)$ if $p=q$, $N_{\mathrm{b}}\dfrac{qe^{(p-q)}+(p-q)e^{-q}-p}{p-q}$ if $p \neq q$
PP	$N_{\mathrm{b}}pq$
CP	$N_{\mathrm{b}}q(e^{p}-1)$
PC	$N_{\mathrm{b}}p(1-e^{-q})$
$P_{\mathrm{A}}(i)$:	
•C	$\sum_{k=i+1}^{n}\left(\left[\left(e^{-\Sigma_{m=i+1}^{k-1}q_m}\right)(1-e^{-q_k})\right]\left\{1-\left(e^{-\Sigma_{m=i+1}^{k-1}r_m}\right)[1-P_{\mathrm{D\mid bL}}(k)]\right\}\right)+\left(e^{-\Sigma_{k=i+1}^{n}q_k}\right)\left\{1-\left(e^{-\Sigma_{k=i+1}^{n}r_k}\right)[1-P_{\mathrm{A}}(n)]\right\}$
•P	$\sum_{k=i+1}^{n}\left(\left(\prod_{m=i+1}^{k-1}1-q_m\right)(q_k)\left\{1-\left(e^{-\Sigma_{m=i+1}^{k-1}r_m}\right)[1-P_{\mathrm{D\mid bL}}(k)]\right\}\right)+\left[\prod_{k=i+1}^{n}(1-q_k)\right]\left\{1-\left(e^{-\Sigma_{k=i+1}^{n}r_k}\right)[1-P_{\mathrm{A}}(n)]\right\}$
$P_{\mathrm{B}}(i)$:	
C•	$\sum_{k=1}^{i-1}\left(\left[\left(e^{-\Sigma_{m=k+1}^{i-1}p_m}\right)(1-e^{-p_k})\right]\left\{1-\left(e^{-\Sigma_{m=k+1}^{i-1}r_m}\right)[1-P_{\mathrm{D\mid Ft}}(k)]\right\}\right)+\left(e^{-\Sigma_{k=1}^{i-1}p_k}\right)\left\{1-\left(e^{-\Sigma_{k=1}^{i-1}r_k}\right)[1-P_{\mathrm{B}}(1)]\right\}$
P•	$\sum_{k=1}^{i-1}\left(\left(\prod_{m=k+1}^{i-1}\dfrac{1}{1+p_m}\right)\left(\dfrac{p_k}{1+p_k}\right)\left\{1-\left(e^{-\Sigma_{m=k+1}^{i-1}r_m}\right)[1-P_{\mathrm{D\mid Ft}}(k)]\right\}\right)+\left(\prod_{k=1}^{i-1}\dfrac{1}{1+p_k}\right)\left\{1-\left(e^{-\Sigma_{k=1}^{i-1}r_k}\right)[1-P_{\mathrm{B}}(1)]\right\}$
$P_{\mathrm{D\mid bt}}$:	
••	$1-e^{-r}$
$P_{\mathrm{D\mid bL}}$:	
•C[b]	$\dfrac{[r+qe^{-(q+r)}]/(q+r)-e^{-q}}{1-e^{-q}}$
•P	$1-e^{-r}$
$P_{\mathrm{D\mid Ft}}$:	
C•[c]	$\dfrac{[r+pe^{-(p+r)}]/(p+r)-e^{-p}}{1-e^{-p}}$
P•	$1-e^{-r}$
$P_{\mathrm{D\mid FL}}$:	
CC[d]	$\dfrac{N_{\mathrm{b}}p}{N_{\mathrm{FL}}}\left\{\dfrac{r}{p+r}-\dfrac{1-e^{-p}}{p}-\dfrac{p[1-e^{-(p+r)}]}{(p+r)^2}\right\}$ if $p=q$, $\dfrac{N_{\mathrm{b}}}{N_{\mathrm{FL}}}\left\{\dfrac{pr[e^{(p-q)}-1]}{(q+r)(p-q)}+\dfrac{pqe^{-(q+r)}[e^{(p+r)}-1]}{(p+r)(q+r)}-e^{-q}(e^{p}-1)\right\}$ if $p \neq q$
PP	$1-e^{-r}$
CP[e]	$\dfrac{r(e^{p}-1)+p(e^{-r}-1)}{p(r+p)(e^{p}-1)}$
PC[f]	$\dfrac{r(e^{q}-1)+q(e^{-r}-1)}{q(r+q)(e^{q}-1)}$

Note. In the two-character code for model, the first character denotes origination and the second extinction; C = continuous, P = pulsed. A bullet means the expression applies to either model for the corresponding process. N_b is the true standing diversity at the start of the interval; because all relevant numbers scale to N_b, this can be arbitrarily set to unity.

[a] Foote 2000*a*, eqq. (6b) and (6c).

[b] Foote 2000*a*, eq. (27b).

[c] Foote 2000*a*, eq. (28b).

[d] Foote 2000*a*, eqq. (29b) and (29c).

[e] Let z represent time within an interval of duration t, where $z=0$ and $z=t$ are the beginning and end of the interval, respectively. By assumption, there is no extinction until the end of the interval. Thus, the density of origination at time z is equal to $e^{pz}/(e^{pt}-1)$ (cf. Foote 2001*a*, eq. [3]). Because all lineages originating within the interval extend to the end, the probability of preservation, given origin at z and extinction at t, is equal to $1-e^{-r(t-z)}$. It is necessary to integrate the density of origination times the probability of preservation over all values of z. Thus, $P_{\mathrm{D\mid FL}}=[1/(e^{pt}-1)]\int_0^t e^{pz}[1-e^{-r(t-z)}]dz$, which is equal to the expression in the table once t is set to unity.

[f] Derived as in the foregoing footnote, with origination and extinction reversed.