Maximum likelihood estimation of phylogeny using stratigraphic data

John P. Huelsenbeck and Bruce Rannala

Abstract.—The stratigraphic distribution of fossil species contains potential information about phylogeny because some phylogenetic trees are more consistent with the distribution of fossils in the rock record than others. A maximum likelihood estimator of phylogeny is derived using an explicit mathematical model of fossil preservation. The method assumes that fossil preservations within lineages follow an independent Poisson process, but can be extended to include other preservation models. The performance of the method was examined using Monte Carlo simulation. The performance of the maximum likelihood estimator of topology increases with an increase in the preservation rate. The method is biased, like other methods of phylogeny estimation, when the rate of fossil preservation is low; estimated trees tend to be more asymmetrical than the true tree. The method appears to perform well as a tree rooting criterion even when preservation rates are low. We suggest several possible extensions of the method to address other questions about the nature of fossil preservation and the process of speciation and extinction over time and space.

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Introduction

Paleontologists have long understood that phylogenies should be congruent with the order of appearance of fossils in the rock record (Gauthier et al. 1988; Norell and Novacek 1992; Benton 1995; Benton and Storrs 1996) and that information about phylogeny is contained in the distribution of fossiliferous horizons for fossil species (Harper 1976; Gingerich 1979; Fisher 1982, 1988, 1991, 1992; Marshall 1990; Huelsenbeck 1994; Wagner 1995). Although at first it may seem counterintuitive that phylogeny can be estimated without any information on morphological or molecular characters (except those characters used to assign fossil specimens to species), the order in which species appear in the fossil record contains information about topology because some topologies imply more missing time (nonpreservation) over the entire tree than do others (Fisher 1992). That is, some phylogenetic trees are more consistent with the temporal distribution of fossil horizons (Fig. 1A). Several methods have been proposed to either estimate topology or measure the fit of the stratigraphic record to phylogenetic trees (Fisher 1992; Gingerich 1979; Gauthier et al.

1988; Huelsenbeck 1994). However, these methods are without a strong statistical justification. Here, we describe a maximum likelihood method to estimate the phylogenetic tree and the speciation and extinction times using stratigraphic information for a collection of fossil species.

Poisson Process Preservation Model

Statistical estimation of phylogeny using stratigraphic data depends upon a model of preservation specifying the probability of observing a given distribution of fossil horizons for a species. In this paper, we consider a very simple model of preservation—the Poisson process model. The parameters of this model are estimated using the maximum likelihood criterion (Edwards 1992); that is, the topology and node times that maximize the probability of observing the data are chosen as best estimates. Although in this paper we consider only a simple Poisson process model of the preservation process, other models can also be developed.

The realized speciation and extinction process is described using a rooted bifurcating tree with the times specified at which speciation and extinction events occur. The topology (τ) and node times are treated as parameters
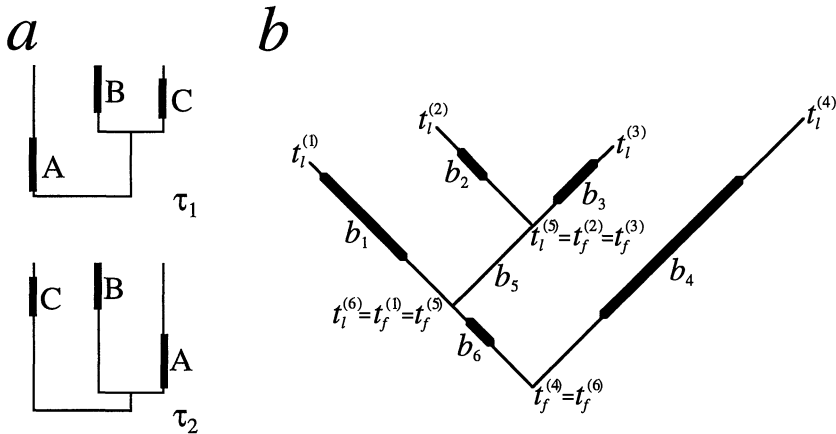
FIGURE 1. The occurrence of fossils in the rock record provides information on phylogeny. Observed stratigraphic ranges of fossil species are denoted as thickened edges on the trees. A, The topology τ_1 provides a better fit to the stratigraphic record than τ_2 because it implies less time with no fossil preservations. B, We treat topology (τ) and node times (t_f and t_l) as parameters of the preservation model.

of the model (Fig. 1B). The node times of the topology specify the actual speciation and extinction times for the ith lineage ($t_f^{(i)}$ and $t_l^{(i)}$, respectively). Each fossil species included in the analysis represents a single lineage. Associated with the ith fossil lineage is a first occurrence ($o_f^{(i)}$) and a last occurrence ($o_l^{(i)}$) in the rock record, and a total number of fossil horizons for that species ($n_o^{(i)}$), including the first and last occurrence. Note that

$$t_f^{(i)} \leq o_f^{(i)} \leq o_l^{(i)} \leq t_l^{(i)}$$

for all $i = 1, \ldots, s$ (where s is the number of lineages) because the first occurrence of a fossil species in the rock record will overestimate the actual speciation time, and the last occurrence will underestimate the actual extinction time.

The rate of preservation of lineages in the rock record over time is assumed to be constant and is therefore described using a Poisson process with preservation rate λ. A Poisson process has been used previously to model fossil preservations (Strauss and Sadler 1989; Marshall 1991) and provides a useful starting point for the analysis of stratigraphic ranges. The joint probability of observing $o_f^{(i)}$, $o_l^{(i)}$ and $n_o^{(i)}$ for the ith lineage is derived by multiplying the probability a particular pair of first and last occurrences are observed conditioned on $n_o^{(i)}$, by the probability that $n_o^{(i)}$ fossil horizons are observed

over the entire lineage. We consider three cases of preservation of a fossil species: (Case 1) when $n_o \geq 2$; (Case 2) when $n_o = 1$; and (Case 3) when $n_o = 0$. In estimating node times and topology, we need to account for cases in which there are no observations for a lineage, as well as those in which there is a single observation. Phylogenetic trees will often imply that some of the taxa were not preserved in the fossil record; we refer to these as "ghost taxa" (Norell 1992).

Case 1.—By a standard result (see Johnson et al. 1994) the distribution of fossil horizons, conditioned on n_o, has a uniform distribution on the interval $[t_f, t_l]$. Considering a single lineage, we may derive a sufficient statistic for estimating t_f and t_l using the joint density of the first and last observations for a collection of independent and identically distributed uniform random variables on the interval $[t_f, t_l]$. These are the smallest and largest order statistics and their distribution may be derived using standard methods to obtain

$$f(o_f, o_l \mid n_o, t_f, t_l)$$
$$= \left(\frac{1}{(t_l - t_f)}\right)^{n_o} n_o(n_o - 1)(o_l - o_f)^{n_o-2} \quad (1)$$

The density $f(n_o \mid t_f, t_l, \lambda)$ under the model is Poisson with parameter $\lambda(t_l - t_f)$ and the joint density of $f(o_f, o_l, n_o \mid t_f, t_l, \lambda)$ is then

$$f(o_f, o_l, n_o | t_f, t_l, \lambda)$$

$$= f(o_f, o_l | n_o, t_f, t_l) f(n_o | t_f, t_l, \lambda)$$

$$= \frac{(o_l - o_f)^{n_o - 2} \lambda^{n_o} e^{-\lambda(t_l - t_f)}}{(n_o - 2)!} \quad (2)$$

Case 2.—With a single observation, the first and last observed occurrences are identical ($o_f = o_l = o$). The probability density for o, using a uniform distribution, is

$$f(o | n_o = 1, t_f, t_l) = \frac{1}{(t_l - t_f)} \quad (3)$$

The probability $f(o, n_o = 1 | t_f, t_l, \lambda)$ can be obtained as in equation 2:

$$f(o, n_o = 1 | t_f, t_l, \lambda) = \lambda e^{-\lambda(t_l - t_f)} \quad (4)$$

Case 3.—The probability that we observe no fossils for a lineage is just the probability of zero observations for a Poisson distribution with parameter $\lambda(t_l - t_f)$.

Likelihood Estimation

The maximum likelihood estimate of a parameter is that value of the parameter for which the probability of observing the data is maximized. Assuming independence of the preservation process over lineages, the likelihood function is

$$L(\tilde{o}_f, \tilde{o}_l, \tilde{n}_o | \tau, \tilde{t}_f, \tilde{t}_l, \lambda)$$

$$= \prod_{i=1}^{s} f(o_f^{(i)}, o_l^{(i)}, n_o^{(i)} | t_f^{(i)}, t_l^{(i)}, \lambda) \quad (5)$$

where the product is over all s lineages of a topology (τ), $\tilde{o}_f = o_f^{(1)}, \ldots, o_f^{(s)}$, $\tilde{o}_l = o_l^{(1)}, \ldots, o_l^{(s)}$, $\tilde{t}_f = t_f^{(1)}, \ldots, t_f^{(s)}$, $\tilde{t}_l = t_l^{(1)}, \ldots, t_l^{(s)}$, and $\tilde{n}_o = n_o^{(1)}, \ldots, n_o^{(s)}$. The maximum likelihood estimates of the parameters of the model of fossil preservation (i.e., the tree topology, node times, and rate of preservation) are determined by maximizing the likelihood function. The likelihood function can be numerically maximized to estimate the topology and node times.

Properties of the Method

For a specific topology, the likelihood is maximized when the range extensions implied by the topology and divergence times are minimized. This property of the method
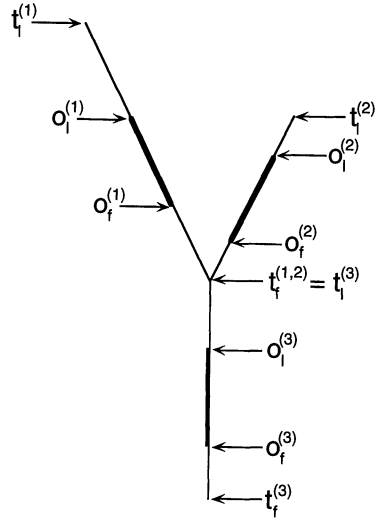
FIGURE 2. A simple three-lineage tree with observed taxon ranges indicated by bold lines. $o_f^{(i)}$ is the observed first occurrence of lineage i and $o_l^{(i)}$ is the observed last occurrence of lineage i. $t_f^{(i)}$ is the speciation time of lineage i and $t_l^{(i)}$ is the extinction time. The log likelihood is proportional to $\log L \propto -\lambda\{(t_l^{(1)} - t_f^{(1,2)}) + (t_l^{(2)} - t_f^{(1,2)}) + (t_f^{(1,2)} - t_f^{(3)})\}$. The constraints on the parameters are $t_l^{(1)} \geq o_l^{(1)}$, $t_l^{(2)} \geq o_l^{(2)}$, $t_f^{(1,2)} \leq \min\{o_f^{(1)}, o_f^{(2)}\}$, $t_l^{(3)} \geq o_l^{(3)}$, $t_f^{(1,2)} \geq o_l^{(3)}$, and $\lambda > 0$. The likelihood is maximized when $t_l^{(1)} = o_l^{(1)}$, $t_l^{(2)} = o_l^{(2)}$, $t_f^{(3)} = o_f^{(3)}$, and $t_f^{(1,2)} = \min\{o_f^{(1)}, o_f^{(2)}\}$.

can best be understood by considering a single lineage. For a single lineage, the probability of observing $o_f^{(i)}$, $o_l^{(i)}$, and $n_o^{(i)}$ is given by equation 2. This function is maximized when the difference in time between the true speciation and extinction times is minimized (i.e., when these are set equal to the observed first and last occurrences, respectively). For a phylogenetic tree of many lineages, the likelihood is maximized when the times at the terminal tips (i.e., extinction times) are as small as possible and the internal node times (i.e., speciation times) are as large as possible. For the entire tree, then, the likelihood is maximized when the missing time implied by a phylogeny is minimized. This is illustrated in Figure 2. The node time estimates on the tree are biased, but consistent (i.e., as the number of fossil horizons increases, the estimates of divergence times converge to their true values).

Fisher's stratigraphic parsimony method chooses that tree which minimizes the number of unobserved stratum crossings (Fisher 1992) as the best estimate of phylogeny. This criterion is similar in spirit to maximum likelihood

implemented with a Poisson process model of fossil preservation. In a sense, our results provide a statistical justification for Fisher's procedure. However, it remains unclear what assumptions are being made by the stratigraphic parsimony method. Also, for reasons that are discussed below, likelihood provides a means for additional hypothesis testing, which is lacking with stratigraphic parsimony.

We used Monte Carlo simulation to examine the accuracy of the maximum likelihood procedure for topology estimation and stratigraphic rooting. Trees were generated under a birth-death model of cladogenesis (Kendall 1949; Raup 1985) in which the speciation rate (α) was twice the extinction rate (μ) ($\alpha = 2.0$, $\mu = 1.0$). Trees were generated over a time interval, T, and preservation events were placed on each simulated tree according to a Poisson process with rate λ. Only trees for which seven lineages (or edges) were represented by fossils were retained. The time interval over which trees were generated (T) was varied for different values of λ in such a way that the expected number of preserved lineages was approximately seven.

Figure 3A shows the efficiency of the maximum likelihood estimator of topology when the preservation rate (λ) is increased. Efficiency was measured by the number of correct components or taxon bipartitions on the estimated tree (a component is determined by that set of taxa on either side of an internal branch of the unrooted tree). There are a total of four components for an unrooted topology of seven species. The maximum likelihood tree was found by an exhaustive search of all possible rooted topologies. As expected, the likelihood method is quite accurate when the preservation rate is high; the performance of the method deteriorates as the fossil record becomes more fragmentary (i.e., λ is small). This suggests the maximum likelihood estimator will perform best for groups with a dense fossil record, such as shelly invertebrates, rather than ones with a poor fossil record, such as many terrestrial vertebrates (Raup and Stanley 1971; Foote and Raup 1996)

The likelihood method using stratigraphic information, like other methods of phyloge-
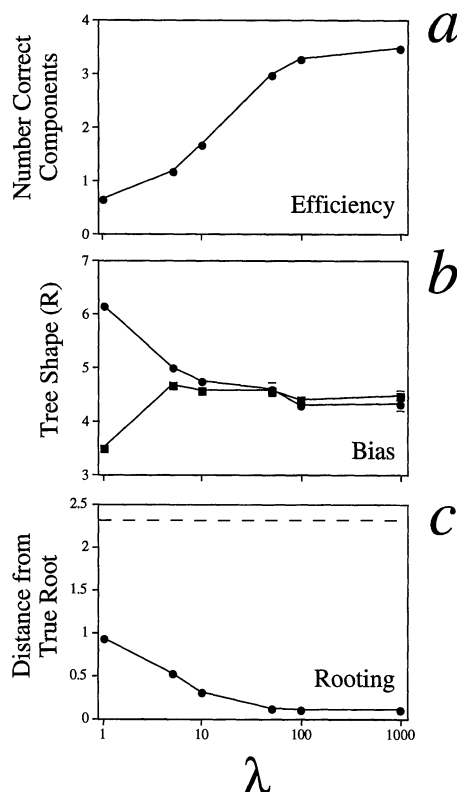

FIGURE 3. The performance of likelihood estimation of topology and node times when the preservation rate (λ) varies. Trees were generated under a birth-death model of cladogenesis in which the speciation rate (α) was twice the extinction rate (μ) ($\alpha = 2.0$, $\mu = 1.0$). A, The efficiency of maximum likelihood estimation of topology when preservation rate (λ) increases. B, The shape (unlabeled rooted topology) of the true (●) versus estimated (■) topologies. Tree shape was measured using Furnas's (1984) left-light rooted index (R). C, The distance of the estimated root from the true root for the stratigraphic rooting criterion. Distance was measured on the correct tree by the number of nodes that must be passed on a direct path from the estimated root to the true root. The dashed line indicates the distance from the true root that would be expected if a random branch were chosen as the root.

netic inference (Huelsenbeck and Kirkpatrick 1996), produces estimated trees that are biased towards asymmetric shapes; this bias decreases as the number of fossil horizons increases (Fig. 3B). Figure 3B plots the shape (unlabeled rooted topology) of the true versus estimated topologies. Tree shape was measured using Furnas's (1984) left-light rooted index (R); trees with small values of the index are more asymmetric than trees with large values. It is interesting to note that although trees were generated under a random branch-

ing model of cladogenesis, the expected tree shape (R) is different from the values when only living taxa are considered ($E(R) = 7.4$ [Kirkpatrick and Slatkin 1993]) because direct ancestors are often included in the samples for these simulations.

The likelihood method performs well as a criterion for rooting a phylogenetic tree, even when the fossil record is very incomplete. Figure 3C plots the distance of the estimated root (based on the stratigraphic data) from the true root. Distance was measured in terms of the number of nodes that must be passed on a direct path from the estimated root to the true root. Only the correct unrooted tree was considered in this analysis and the likelihood of each possible root position was calculated; the position with the highest likelihood was used as the root estimate. The dashed line in Figure 3C indicates the distance from the true root that would be expected if a random branch were chosen as the root.

Extensions of the Method

Several applications of stratigraphic information to evolutionary questions have been suggested previously (reviewed in Huelsenbeck 1994). These applications include estimating phylogeny, determining the root of a phylogenetic tree, and examining the agreement between a phylogenetic tree and the stratigraphic record. Because the stratigraphic record is limited for most groups and the estimates of phylogeny using stratigraphic methods are biased for low preservation rates, stratigraphic methods may not be best suited for estimating phylogeny without additional data from other sources. However, the simulation results of this study suggest that stratigraphic data can provide valuable information on the position of the root of a tree. There are several other possible applications of a likelihood approach using stratigraphic data, which we outline below.

Likelihood Ratio Test of Preservation Models.— The likelihood of the observed stratigraphic record can potentially be calculated using other models of preservation, including models that do not assume independent preservations among lineages (e.g., a compound Poisson model of preservation) or a discrete time mod-

el of preservation (e.g., Foote and Raup 1996). The fit of alternative preservation models can be evaluated using likelihood ratio tests. The likelihood ratio test statistic for comparing two models (Λ) is defined as

$$\Lambda = \frac{\max[L(\text{Model A}) \,|\, (\text{Stratigraphic Data})]}{\max[L(\text{Model B}) \,|\, (\text{Stratigraphic Data})]}$$

(6)

The ratio of the likelihoods calculated under the null and alternative models (models A and B, respectively) is a measure of the relative merit of each. If Λ is less than one, then the alternative model is favored. If Λ is greater than one, the null model is favored. For the special case of nested models, $\Lambda < 1$ and $-2\log\Lambda$ is asymptotically χ^2 distributed under the null model with q degrees of freedom, where q is the difference in the number of parameters between the general and restricted models (Cox and Hinkley 1974). The null distribution of the likelihood ratio test statistic can also be determined using simulation under the null model with maximum likelihood estimates substituted for the true parameters. That is, parameter estimates under the null model (topology, branch lengths, and the preservation rate) are used to generate many independent data sets using Monte Carlo simulation. For each simulated data set, the test statistic is calculated. If the observed test statistic is greater than some predetermined proportion of the simulated test statistics (usually 95%), then the null model is rejected. This parametric bootstrap procedure does not require models to be nested and is widely used in statistics (Cox 1961, 1962).

Did Two or More Lineages Simultaneously Speciate or Go Extinct?—Solow (1996) considered a test of the null hypothesis that two or more species went extinct at the same time using a likelihood ratio test and a Poisson process model of fossil preservation. Because Solow (1996) only considered the null model of contemporaneous extinction, his model did not incorporate information on phylogeny. However, null hypotheses of lineage origin or extinction can be tested in a phylogenetic framework using the model presented in this paper. The likelihood under the null hypothesis (L_0)

can be calculated with the constraint that all species originated, or disappeared, at the same time. This null hypothesis corresponds to a scenario in which a mass extinction was followed by rapid speciation. The constraints of identical originations or extinctions are relaxed when calculating the likelihood under the alternative hypothesis (L_1). The significance of the likelihood ratio test statistic ($\Lambda = L_0/L_1$) is determined using parametric bootstrapping.

Combining Stratigraphic and Character Data.—One problem that arises when using stratigraphic data in a phylogenetic analysis that includes other types of data (such as morphological or molecular data) concerns how much weight the stratigraphic data should receive. For the stratigraphic parsimony method, the "stratigraphic parsimony debt" (minimum number of stratum crossings implied by a topolology) and "parsimony debt" (minimum number of character state changes implied by a topology) are summed (Fisher 1992). However, the weight the stratigraphic data receive can be arbitrarily increased or decreased by considering more or fewer stratigraphic horizons, respectively. Likelihood suggests a rational means of combining diverse data. If the data from morphology, molecules, and stratigraphy are independent, then the overall likelihood is the product of the likelihoods calculated for each type of data (or, equivalently, the overall log likelihood is the sum of the log likelihoods for each type of data). Although it is currently possible to calculate likelihoods for molecular and stratigraphic data, calculating likelihoods for morphological data is problematic. However, we note that a Brownian motion model, as implemented in Felsenstein's program CONTML (Felsenstein 1995), can be used to estimate phylogeny for continuously varying characters.

Confidence Intervals on Node Times.—Confidence intervals on the parameter estimates (node times and preservation rate, λ) for a given topology can be calculated by taking advantage of large sample theory for maximum likelihood estimates. For large samples, the distribution of a maximum likelihood estimate ($\hat{t}$) is approximately normal with mean t

and variance $1/nI(t)$, where t is the true value of the parameter, n is the observed number of preservations, and $I(t)$ is Fisher's information, defined as

$$I(t) = E\left[\frac{\partial}{\partial t} \log f(X \mid t)\right]^2$$

where $f(X \mid t)$ is the probability distribution for the data and E denotes the expectation. Under appropriate smoothness conditions, the distribution of $\sqrt{nI(t)}(\hat{t} - t)$ tends to a standard normal distribution with increasing n. Hence, the α-level confidence interval for parameter t can be approximated as $\hat{t} \pm z(\alpha/2) \, 1/\sqrt{nI(t)}$ where z is a standard normal distribution.

Discussion

A model-based approach, as presented in this paper, provides a set of well-defined procedures for estimating phylogenetic trees using data from the stratigraphic record. It also opens a new area of research to taphonomists interested in the process of fossil preservation. By evaluating alternative models, one can determine whether adding a parameter to a mathematical model of preservation provides a significant improvement in the fit of the model to the data. An analogous research program was established in molecular evolution less than a decade ago in which models of DNA substitution were examined. This approach has allowed molecular evolutionists to compare and test models that account for base substitution biases (Goldman 1993), among-site rate variation (Yang 1993), differences in underlying topology for different data partitions (Huelsenbeck and Bull 1996), and non-clock-like behavior of the substitution process (Felsenstein 1981). The preservation model we present in this paper is very simple. Future work should concentrate on devising more realistic models of preservation and testing these models using likelihood ratio tests.

The relative efficiencies of the maximum likelihood estimator of topology and node times developed in this paper, as well as of other stratigraphic methods (e.g., Fisher 1992), are presently unknown. However, the preliminary simulations performed in this paper suggest that it may be possible to estimate to-

pology accurately using our method. A thorough study examining the statistical properties of phylogenetic methods using stratigraphic data should help determine the relative strengths and weaknesses of the different methods. Simulations should prove particularly useful for such comparisons.

Acknowledgments

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