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Modelling rate distributions using character compatibility: implications for morphological evolution among fossil invertebrates

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Rate distributions are important considerations when testing hypotheses about morphological evolution or phylogeny. They also have implications about general processes underlying character evolution. Molecular systematists often assume that rates are Poisson processes with gamma distributions. However, morphological change is the product of multiple probabilistic processes and should theoretically be affected by hierarchical integration of characters. Both factors predict lognormal rate distributions. Here, a simple inverse modelling approach assesses the best single-rate, gamma and lognormal models given observed character compatibility for 115 invertebrate groups. Tests reject the single-rate model for nearly all cases. Moreover, the lognormal outperforms the gamma for character change rates and (especially) state derivation rates. The latter in particular is consistent with integration affecting morphological character evolution.

Keywords: character evolution; compatibility; lognormal distribution; gamma distribution; information theory

1. INTRODUCTION

Palaeontologists are interested in rates of character state change both for testing macroevolutionary hypotheses and for inferring phylogeny. However, palaeontologists have paid much more attention to rate variation over time and among clades than to rate variation among characters. Indeed, most rate and systematic studies tacitly assume a single rate for all characters. We have not yet explored whether there are any general rules for rate distributions, or even whether single-rate models are poor ones.

Molecular systematists often model rate variation with gamma distributions. This assumes a collection of Poisson processes with different 'waiting times' between events [1]. However, palaeontologists use only fossilizable morphology. Morphological change is probably the product of waiting time and probabilistically

varying selective forces. Moreover, biomechanics, development and genetics probably create hierarchical interactions among morphological characters [2]. Rates for any one character thus should partially reflect both the number of associated characters and the probabilities of those characters accommodating a change. If overall rates are products of independent probabilistic processes [3] and/or hierarchical linkages [4], then morphological rates should fit lognormal distributions.

Palaeontologists have combined simulations with the morphological disparity of character matrices to assess general rates of change (e.g. [5]). Systematists have used the related concept of compatibility to contrast general rates for individual characters (e.g. [6]) (see the electronic supplementary material for a contrast of disparity and compatibility). Here, I unite both traditions to assess how well three basic models of character evolution (single rates, gamma distributions and lognormal distributions) predict fossil morphologies.

2. MATERIAL AND METHODS

(a) Compatibility, steps and rates

Yang [1] suggests using steps implied by parsimony trees to establish rate distributions. However, when simulated matrix structure matches that of real data, parsimony steps blur rate classes [7]. Instead, I use character compatibility to approximate steps. A compatible character pair has no necessary homoplasy: a binary pair combining for 00, 01 and 11 might not have homoplasy but a pair also including combination 10 must have homoplasy [6,8]. Simulations corroborate the suggestion that compatibility decreases as frequencies of change (and homoplasy) increase, both for whole matrices [7] and for individual characters [9].

State distributions also affect the probability of compatibility. Suppose two binary characters change only once. For character A, only one taxon possesses state 1. State 1 cannot be paired with two states in any other character, and thus cannot create incompatibility. Conversely, character B changes in the middle of the phylogeny so that half of the taxa have state 0 and other half have state 1. Both states 0 and 1 for character B now have four opportunities to be paired with a second state for other binary characters. In simulations, compatibility given X steps decreases as states become more 'evenly' distributed among taxa (see electronic supplementary material).

This study uses simulations to inversely model the probability of observed compatibilities and state distributions given the rates of character state change. For a clade of S taxa with N_{ch} characters, each simulation:

— evolves a tree of S taxa;
— evolves N_{ch} characters (retaining the observed state numbers and missing entries as the data) until the observed compatibility is reached;
— iteratively removes simulated characters matching the compatibility of observed characters;
— re-simulates the 'matching' character with $1, \ldots, S$ steps; and
— tallies how often we find observed compatibility and state distributions given $1, \ldots, S$ steps.

There are three critical differences between this approach and permutation tests assessing character compatibilities (e.g. [10–12]). First, phylogeny underlies the character state distributions even under high rates of change (part 1). Second, each character is compared with a 'remaining' matrix having the same compatibility as the observed 'remaining' matrix (parts 2 and 3). Finally, results are tied to specific amounts of change (parts 4 and 5).

Now, we have the likelihoods of $1, \ldots, S$ changes (steps) given the observed compatibility for each character. However, model evaluation requires numbers of characters with X steps (see below). This, in turn, requires posterior probabilities rather than likelihoods. Assuming flat priors for step numbers, the probability of character C having X steps is:

$$\frac{p[\text{compatibility of C}|X \text{ steps}]}{\sum_{Y=1}^{S} p[\text{compatibility of C}|Y \text{ steps}]}.$$
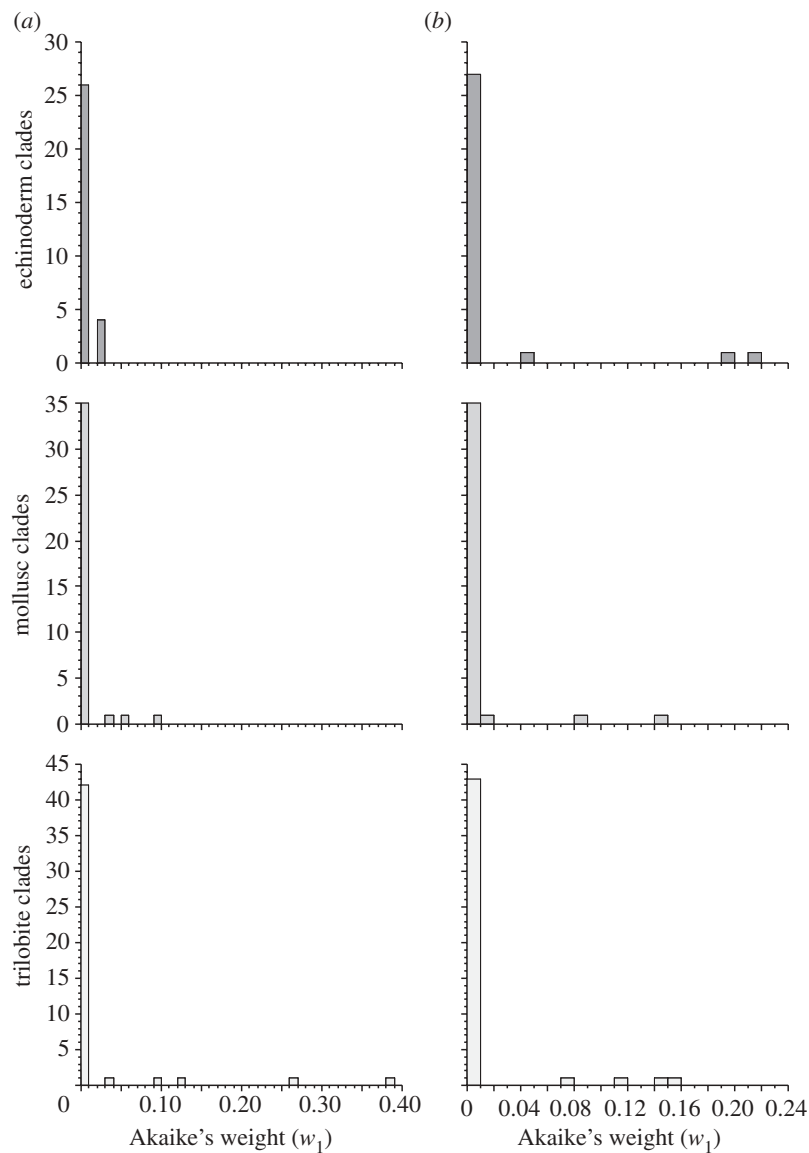
Figure 1. Akaike's weights (w_1) for single-rate models of (a) character change and (b) state derivation. These are akin to Bayesian probabilities that the model is the most correct of the models considered.

The estimated number of characters with X steps now is:

$$\sum_{C=1}^{N_{ch}} p[X \text{steps} | \text{compatibility of C}].$$

Character evolution models, such as the Mk model [13], describe rates of character change *and* rates of state derivation. This distinction is critical when characters have different numbers of states. Consider simple transition matrices for two-state character A and a three-state character B, where the off-diagonals give p[state derivation] and the diagonal gives p[stasis] (i.e. $1 - p$[change δ]):

$$
\begin{array}{cccc}
\text{states} & 0 & 1 \\
0 & 1 - \delta_A & \delta_A \\
1 & \delta_A & 1 - \delta_A
\end{array}
\text{ versus }
\begin{array}{ccccc}
\text{states} & 0 & 1 & 2 \\
0 & 1 - \delta_B & \frac{\delta_B}{2} & \frac{\delta_B}{2} \\
1 & \frac{\delta_B}{2} & 1 - \delta_B & \frac{\delta_B}{2} \\
2 & \frac{\delta_B}{2} & \frac{\delta_B}{2} & 1 - \delta_B
\end{array}.
$$

If $\delta_A = \delta_B$, then the rate of state derivation is necessarily lower for B than for A; conversely, if the rates of state derivation are the same, then $\delta_B = 2\delta_A$. An upshot of this is that rates of character change and rates of state derivation need not fit the same models.

These analyses assume equiprobable state transitions. (The issue of biased-state derivation requires a phylogenetic context, if only to assess the primitive state.) Thus, models are not fitted using how frequently particular states are derived, but how frequently we derive the first or second 'other' state given any ancestral state. There is

at least one derivation for each 'other' state (e.g. the two 'other' states for character B above must be derived once each). At four steps, we have two additional derivations, so for each 'other' state:

p[0 additional derivations] $= p$[2 additional derivations] $= 0.25$;

p[1 additional derivation] $= 0.50$.

As there are two 'other' states, we expect $2 \times 0.25 = 0.50$ states to be derived either once or three times in total, and $2 \times 0.50 = 1.0$ to be derived twice the total. The number of states from each character expected to be derived Y times now is the sum of $p[Y$ derivations $\mid X$ steps$] \times p[X$ steps $\mid$ data$]$ for $X = 1, \ldots, S$. This is summed over all characters. Analyses then use that final summation to evaluate different models (see electronic supplementary material).

(b) Rate distribution models

The single-rate model varies one parameter: mean rate, δ. Gamma distributions use a scale and a shape parameter to vary rates around the mean rate (δ). Following Yang [1], I set the scale equal to shape, which leaves one freely varying parameter. Increasing the size/shape parameter decreases the rate variation. The lognormal uses an order of magnitude increase/decrease given the deviation from the mean rate. Thus, p[rate $= 2\delta] = p$[rate $= \delta/2$]. Thus, both the gamma and lognormals vary two parameters: mean rate (δ) and the distribution parameter. Analyses then divide the distributions into four equal areas [1], with the midpoint of each quadrant used for the rate relative to δ.

Characters are not assigned to particular rate classes. Instead, likelihoods contrast the reconstructed and expected number of characters with $1, \ldots, S$ changes given $N'/4$ characters with rates 1, 2, 3
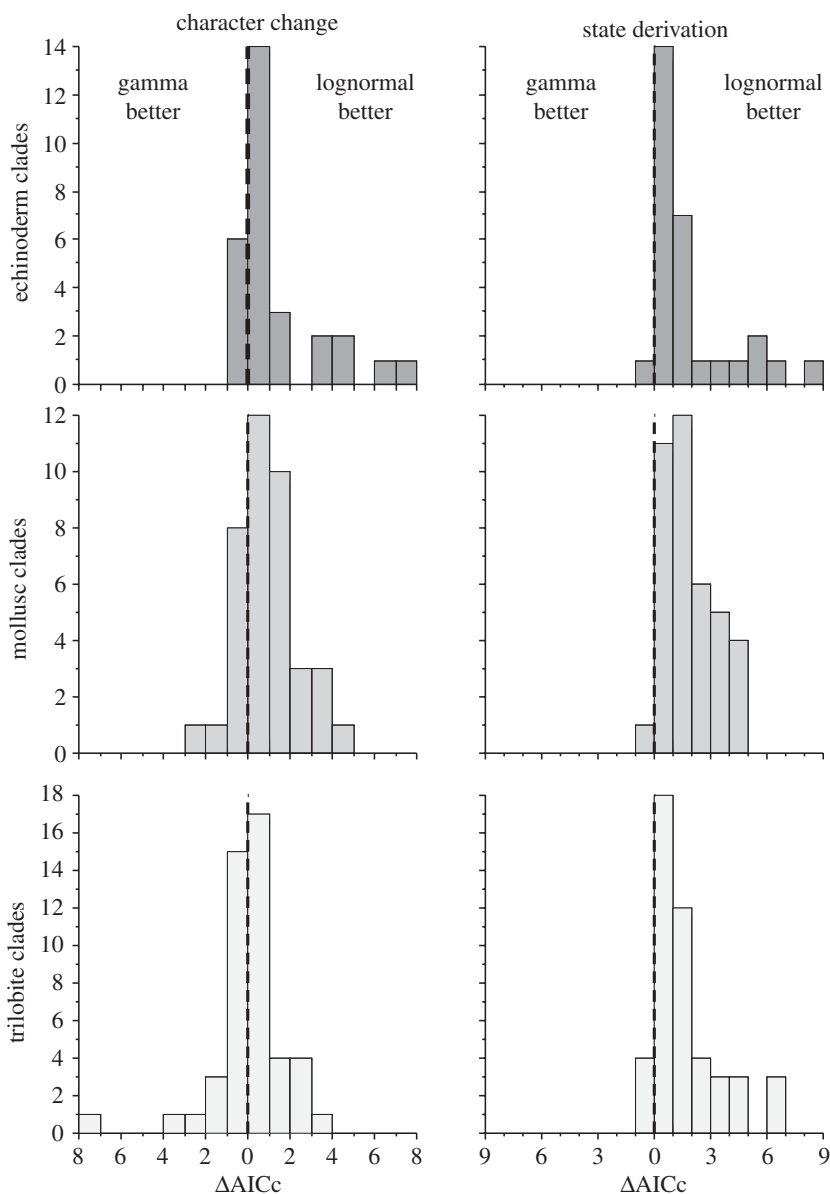
Figure 2. Differences in AICc between lognormal and gamma distributions. Following convention, the numbers are positive on both sides of the *x*-axis.

and 4, where N' is a hypothetical 'true' number of characters including the varying characters (N) plus some invariant ones. Note that N' is an outcome of the best hypotheses rather than a freely varying parameter. The procedure is repeated for state derivations (see electronic supplementary material, appendix A).

Distribution likelihoods are

$$L[\text{rates}|\text{observations}] \propto \sum_{i=1}^{S} f\,[\text{observations}|i\text{ steps}] \times P[i\text{ steps}|\text{rates}].$$

I then use Akaike's modified information criterion (AICc; [14]) to rescale model log-likelihoods given equal parameter and sample size 'efforts' for all three models:

$$\text{AICc} = -2 \ln L[\text{ML hypothesis for model}] + 2K\left(\frac{N}{N-K-1}\right),$$

where K is the number of parameters (1 for single-rate, 2 for lognormal and gamma) and N is the number of data points (i.e. observed characters or derived states). Each model is evaluated by the differences between its AICc and the overall best AICc. For the 'null' single-rate model, I use Akaike's weights [15]:

$$w_i = \frac{e^{-\Delta_{1-\text{rate}/2}}}{\sum_{\text{model}=1}^{3} e^{-\Delta_{1-\text{model}/2}}}.$$

This rescales data probabilities given differences in model parameters and then relative to the sum of rescaled data probabilities

for all three models. I use AICc differences (ΔAICc) to contrast the gamma and lognormal hypotheses.

(c) *Data*

I analyse 115 published character matrices of fossil echinoderms, molluscs and trilobites (see electronic supplementary material, appendix B). For most matrices, I exclude outgroup taxa (especially hypothetical ancestors). Analyses exclude dependent characters, i.e. those describing particular conditions of features absent on some clade members. These require an extra layer of analysis where change is conditioned on the state of a particular independent character. Dependent characters also require allowing for zero steps as two states might reflect two derivations of the independent character. Finally, polymorphic characters are set to states that maximize the compatibility of the character.

3. RESULTS

Single-rate models explain character compatibility patterns poorly relative to distributed rate models (figure 1). Half of the character rate examples have $w_{1\text{Rate}} < 10^{-10}$ and half of the state derivation examples have $w_{1\text{Rate}} < 10^{-9}$.

For rates of character change, the lognormal model outperforms the gamma model in 78 of 115 cases (figure 2). The pattern is much stronger for

echinoderms (23 of 29 cases) and molluscs (29 of 39 cases) than for trilobites (26 of 47 cases). For rates of state derivation, the lognormal performs best across all three groups (108 of 115 cases).

4. DISCUSSION

We can clearly reject the idea of single-rate models of morphological character change for the majority of invertebrate groups examined here. The few cases where we cannot do so use few taxa and/or characters and thus implicate sample size. Allowing for distributed rates might alter interpretations of macroevolutionary studies showing altered mean rates (δ) over phylogeny. For example, δ is lower for derived rostroconchs than for stem rostroconchs [16]. However, these analyses indicate that the shift reflects decreases to the slower rate classes while the highest rates remain little changed (see electronic supplementary material, appendix A).

Basic phylogenetic inference methods (e.g. [17,18]) assume single-rate models of character change. Simulations demonstrate that rate heterogeneity confounds such methods (e.g. [19,20]). Likelihood and Bayesian methods (e.g. MrBayes; [21]) allow distributed rates but currently consider only gamma distributions (e.g. [22]). The extent to which distributed rates in general and lognormal distributions in particular alter phylogenetic inferences of fossil taxa requires examination.

The preponderance of lognormal rate distributions suggests that morphological evolution is more than a collection of Poisson processes. The two explanations, i.e. multiple independent processes and hierarchical linkage/integration, are not mutually exclusive. However, 'independent processes' might best pertain to *when* characters change, whereas 'integration' might best pertain to *how* characters change (state derivation). Of course, rates of state derivation will affect rates of change, and vice versa. However, for several clades, gamma better describes rates of change whereas lognormal better describes rates of derivation. This is particularly true for trilobites (figure 2). This suggests that simple stochastic processes affect *when* change happens, but some other set of rules (such as integration) affect *what* change can occur. Proper testing of these ideas is beyond the scope of this paper. Nevertheless, the dominance of lognormal rate distributions over gamma rate distributions shows that palaeontological data leave more evidence of underlying processes than previously suggested.

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SUPPLEMENT A: METHODS

1. THE BEHAVIOR OF COMPATIBILITY IN SIMULATIONS

The simulations presented here involve 32 taxa with 100 binary characters.

Phylogenies follow an "MBL" style (Raup *et al.* 1973; Raup & Gould 1974)

using origination rate = 0.50, extinction rate = 0.45 and sampling rate =

0.25 per unit time and with morphological change restricted to branching

events. Note that essentially identical results are obtained under different

phylogenetic models (e.g., bifurcation or including only extant taxa) or

under continuous change over time. Finally, note that the general patterns

apply when multistate characters are used instead of binary characters, with

the difference being that more change is required to introduce homoplasy

and thus to reduce compatibility.

(a) Whole matrix compatibility

Wagner (2001) illustrates basic differences between average frequencies of

change and compatibility for matrices modelled on gastropod data. The

simulations here present the general pattern responsible for those results.

As predicted by others (e.g., Estabrook *et al.* 1975; Felsenstein 1981), the

total number of compatible pairs within a matrix declines markedly as the

amount of change (and thus the amount of homoplasy) increases (figure

S1). However, it is also the case that the likelihood surface becomes flatter

as amounts of change increase. This is because compatibility is tied to

sampled homoplasy, and at higher rates of change there is an increase in

reversals along unsampled branches that have no effect on overall

homoplasy or that sometimes even reverse homoplasies so that they are

unsampled.

These results also emphasize why permutation tests for whole matrices (e.g., Alroy 1994; Wilkinson 1994) reject an "overly" null hypothesis. Even at the highest frequencies of change used here, the resulting matrices show more structure than would permuted matrices. However, our ability to reconstruct phylogeny easily from these simulated matrices is much lower for the 250

Figure S1. Relationship between compatibility and numbers of changes among 100 binary characters for 32 taxa based on 10000 simulations per numbers of steps. The maximum possible compatibility is 4950 CPs.

step simulations than for the 150 step simulations. Thus, permutation tests

really would reject only the ideas that there is no underlying phylogeny or

that the characters had evolved at such extremely high rates that all

phylogenetic signal is lost.
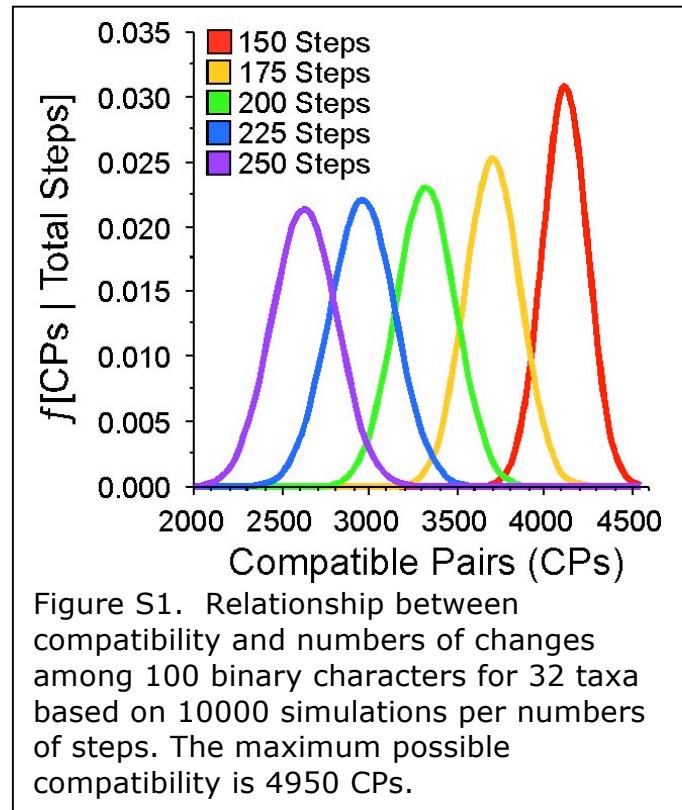
(b) Individual character compatibility

O'Keefe & Wagner (2001) illustrate the basic correlation between numbers of changes and compatibility. However, it is also well-known that individual character compatibility reflects the relative numbers of taxa with different states (e.g., Estabrook *et al.* 1975;


Figure S2. Individual character compatibility. Histograms give compatibilities given 1, 2 or 3 steps, with 175 total steps. The accompanying scatter plot shows the relationship between state distribution and compatibility given 1, 2 or 3 steps. "Minority State Richness" = number of taxa with the less common state.

Sharkey 1989). Figure S2 shows results from a single simulation of 175 steps used above. Histograms show that numbers of changes strongly affect
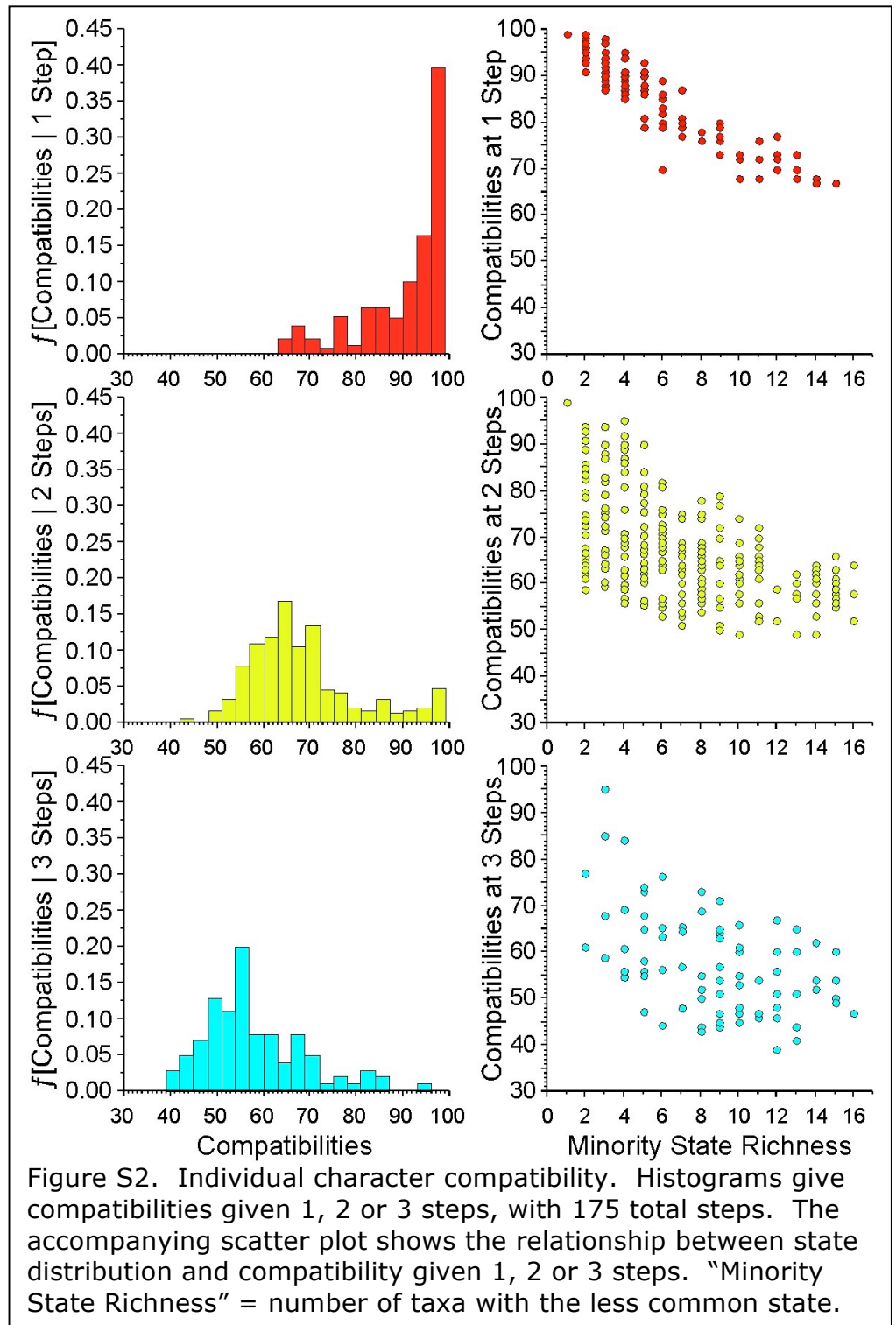
the likelihood. Moreover, the variation in compatibility given 1, 2 or 3 steps

(and especially for 1 step) is strongly affected by the number of taxa with

the "minority" state. For an autapomorphic character, the minority state

richness is 1, with the other 31 taxa showing the other state. (Note that this

could be 31 taxa with state 0 and one with state 1, or one taxon with state 0

and 31 with state 1.)

2. APPROXIMATING NUMBERS OF CHARACTERS WITH X CHANGES

Table 1 provides an example of the output for hippuritoid (rudist) bivalves

based on a study by Stone & Telford (1999). Each entry approximates:

P[observations | St Steps]

For any given rate δ, we now could calculate the likelihood simply as:

$$L[d \mid observations] = \sum_{St=1}^{S} P[observations \mid St] \times P[St \mid \delta]$$

using the values in the cells above. However, as will be made clear in the

Table S1. Step (St) likelihoods for 12 rudist characters (Stone & Telford 1999) given character compatibility. Based on 100000 simulations.

St	01	02	03	04	05	06	07	08	09	10	11	12
1	0.566	0.083	0.000	0.000	0.020	0.000	0.013	0.020	0.085	0.083	0.566	0.006
2	0.041	0.055	0.000	0.014	0.027	0.012	0.007	0.027	0.059	0.055	0.041	0.066
3	0.015	0.011	0.009	0.013	0.022	0.027	0.003	0.022	0.019	0.011	0.015	0.016
4	0.014	0.006	0.008	0.009	0.017	0.013	0.002	0.017	0.009	0.006	0.014	0.007
5	0.006	0.005	0.002	0.005	0.014	0.009	0.001	0.014	0.007	0.005	0.006	0.007
6	0.003	0.003	0.001	0.004	0.010	0.009	0.001	0.010	0.005	0.003	0.003	0.004
7	0.003	0.002	0.001	0.003	0.009	0.008	0.001	0.009	0.003	0.002	0.003	0.003
8	0.002	0.002	0.000	0.002	0.008	0.006	0.001	0.008	0.003	0.002	0.002	0.002
9	0.002	0.002	0.000	0.002	0.007	0.006	0.001	0.007	0.003	0.002	0.002	0.002
10	0.002	0.001	0.000	0.001	0.007	0.006	0.000	0.007	0.002	0.001	0.002	0.002
11	0.001	0.001	0.000	0.001	0.006	0.005	0.000	0.006	0.002	0.001	0.001	0.002
12	0.001	0.001	0.000	0.001	0.006	0.005	0.000	0.006	0.002	0.001	0.001	0.002

next section, the models posit some number of characters with zero

changes, which requires that we condition our probabilities and likelihoods

on expected numbers of observed characters. Instead, we can calculate the

probability that each character if we assume that the prior probability of

each step is equal. Table 2 shows this for the rudist example: each value is

simply rescaled to the sum of the likelihoods for each character.
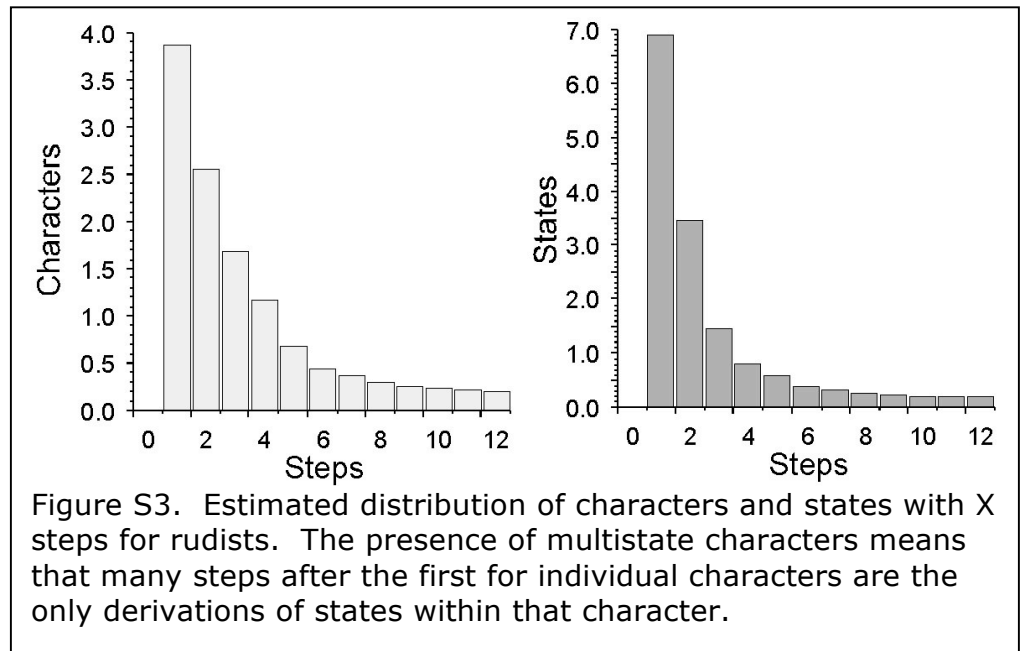
Table 2. Step probabilities for 12 rudist characters given state likelihoods in Table 1 and assuming flat prior probabilities for each step number.

St	01	02	03	04	05	06	07	08	09	10	11	12
1	0.861	0.483	0.000	0.000	0.133	0.000	0.432	0.133	0.426	0.483	0.861	0.050
2	0.062	0.318	0.000	0.257	0.176	0.118	0.229	0.176	0.298	0.318	0.062	0.548
3	0.023	0.064	0.402	0.233	0.145	0.251	0.108	0.145	0.095	0.064	0.023	0.130
4	0.022	0.034	0.394	0.160	0.108	0.122	0.063	0.108	0.044	0.034	0.022	0.061
5	0.010	0.030	0.103	0.098	0.094	0.086	0.040	0.094	0.034	0.030	0.010	0.061
6	0.005	0.018	0.032	0.068	0.067	0.081	0.030	0.067	0.024	0.018	0.005	0.036
7	0.005	0.011	0.027	0.050	0.059	0.075	0.020	0.059	0.017	0.011	0.005	0.023
8	0.003	0.010	0.019	0.042	0.050	0.059	0.020	0.050	0.015	0.010	0.003	0.020
9	0.002	0.009	0.010	0.028	0.044	0.058	0.017	0.044	0.013	0.009	0.002	0.019
10	0.002	0.008	0.007	0.024	0.043	0.054	0.016	0.043	0.012	0.008	0.002	0.018
11	0.002	0.007	0.003	0.020	0.042	0.051	0.013	0.042	0.011	0.007	0.002	0.017
12	0.002	0.007	0.003	0.021	0.039	0.045	0.013	0.039	0.011	0.007	0.002	0.015

Now, we can estimate the "number" of characters that change X times as

the sum of the probabilities that each individual character changes X times.

This leaves the distribution shown on the left in figure S3, which sums to the

number of characters.

        The distribution of state derivations assumes that changes are

distributed with equal probability among the observed character states.

Note that this does *not* focus on particular states. That is, if we have a 3 state character, we do not worry about derivations of states 0, 1 and 2. Instead, we look at how often

Figure S3. Estimated distribution of characters and states with X steps for rudists. The presence of multistate characters means that many steps after the first for individual characters are the only derivations of states within that character.

we would derive the 1st and 2nd alternate states from the current condition.

If a 3-state character shows 2 changes, then it necessarily is 1 derivation

per state. If there are, say, 6 changes, then we have 4 extra derivations to

distribute among the two alternate states. Thus, for each state, the number

of times it changes 0 – 4 extra times (or 1 to 5 in total) is simply the

binomial probability of 0, 1, … 4 of the 4 changes given a probability of 0.5

of achieving any one of those distributions. This is then multiplied by the

probability of the character changing 6 times. Thus, the probability that an

alternative state from a 3-state character was derived 4 times in total is the

sum of the probabilities of 3 "extra" derivations given 5…S total steps

weighted by the probability that there were 5…S total steps. For rudists, this

leaves the distribution shown on the right in figure 3S, which sums to the

total number of derived states (i.e., total states – total characters).

3. DERIVING EXPECTED CHANGES FOR DISTRIBUTED RATE MODELS

Following Yang (1994), I evaluate gamma and lognormal distributions given

4 partitions representing the midpoints of four equal-area partitions of the

relevant distribution. These give 4 "proportional" rates that are multiplied by an average rate to get the expected number of characters or states with 1, 2, etc. changes (figure S4). In the example here, the average character is expected to change twice on
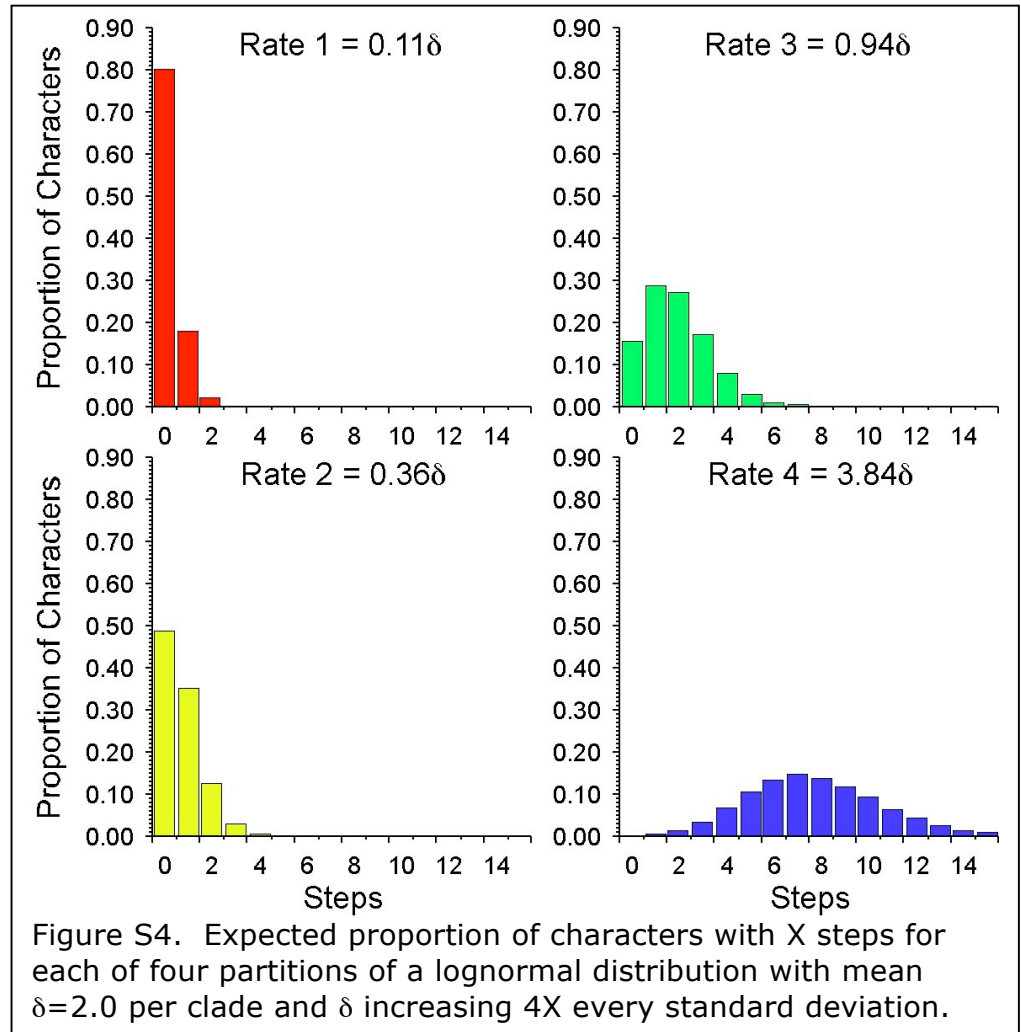

Figure S4. Expected proportion of characters with X steps for each of four partitions of a lognormal distribution with mean $\delta=2.0$ per clade and δ increasing 4X every standard deviation.

the tree ($\delta=2.0$), with each "standard deviation" of the lognormal curve

changing that by 4X. Note that there is substantial overlap between each
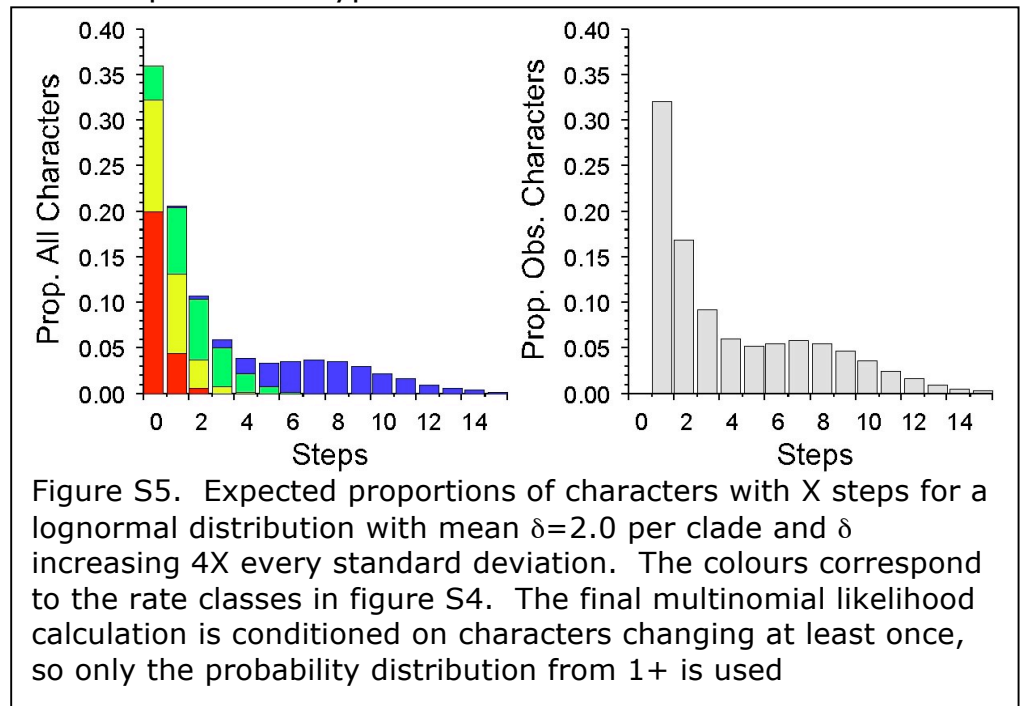
rate class with no specification of which characters should belong to which

rate class.

These four distributions then are averaged (Figure S5). Sensibly, the fast

rate contributes most to expected characters with many changes. As a

corollary, the "slow" rate classes contribute largely to expected proportion of

characters changing infrequently. The two lowest rate classes in particular

posit a number of hypothetical characters that are invariant among the

sampled taxa and thus not "visible" to systematists. Estimating such

characters is important when calculating likelihoods (and thus Bayesian

probabilities) of phylogenies (Lewis 2001). For our purposes here, the

important part of the probability distribution function (pdf) is the relative

proportion of characters with 1, 2, 3, etc., changes. Thus, we condition the

probabilities on the character changing at least once and thus rescale the pdf

to the area by (1-P[0 changes | lognormal]. This is shown in gray in figure

S4. The log-likelihood of this particular hypothesis then is the multinomial

then is the sum of the estimated number of characters with X changes times the log probability of having X changes. In other words, it would be the height

Figure S5. Expected proportions of characters with X steps for a lognormal distribution with mean $\delta=2.0$ per clade and δ increasing 4X every standard deviation. The colours correspond to the rate classes in figure S4. The final multinomial likelihood calculation is conditioned on characters changing at least once, so only the probability distribution from 1+ is used

of the histograms from figure 3S (estimated numbers of characters with X

changes or states with X derivations) times the log of the height of second

histogram in figure 5S.

Finally, it requires emphasizing that the type of likelihoods derived here

could be called "approximate likelihoods" rather than true likelihoods (e.g.,

Beaumont 2010). This is because the tests do not use the exact

probabilities of the exact observations (i.e., distributions of character

states). Instead, these tests use a statistic of the observations (e.g.,

compatibility). This is equivalent to asking the probability of getting the

means or variances within a collection of population given different models

instead of the probability of getting (say) the exact distribution of heights

within those populations.

4. ON THE GENERAL RELATIONSHIP BETWEEN COMPATIBILITY AND DISPARITY

Disparity summarizes the range of morphological variation within a clade

(e.g., Gould 1991). Although the diversity of higher taxa often reflects

disparity, disparity itself provides a repeatable summary of morphological

variation that taxonomic counts alone cannot. More relevant to this work,

workers have thoroughly explored the relationship between disparity and

rates of morphological evolution. For a given number of taxa, characters and

character states, the expected disparity increases as amounts (and thus

rates) of evolution increase (Foote 1991), at least up to some "saturation"

point where maximum possible disparity is realized (Lupia 1999). Moreover,

we also expect disparity to increase as clades with novel morphotypes

diversify, even if the novel morphologies in question do not themselves

further evolve. As shown above, we expect compatibility to decrease under

both conditions.

There are many measures of morphological disparity (see, e.g., Ciampaglio

et al. 2001), but metrics using character data such as used in cladistic

analyses begin with pairwise dissimilarity (e.g., Foote 1992, 1994). That is,

what proportion of the characters are the same between any two taxa? One

can understand the general relationship between pairwise dissimilarity and

compatibility with single character vectors. Suppose that we have binary

characters for a 10-taxon clade:

  Character A: 0 0 0 0 0 0 0 0 0 1

  Character B: 0 0 0 0 0 1 1 1 1 1

For 10 taxa, there are 45 pairwise comparisons. For Character A, 9 of them

have a difference of 1 and the remaining 36 have a difference of 0. Thus,

the average pairwise dissimilarity for this character alone is $\frac{9}{45}=0.20$.

Character A also must be compatible with every other character, even if

those other characters are highly homoplastic. To be incompatible with

another binary character, we need to see 00, 01, 10 and 11. However,

because Character A has only a single taxon with State 1, it is impossible to

see both 10 and 11. So, minimizing the disparity from a variable character

maximizes its compatibility.

Conversely, Character B has an even split of 5 taxa each with States 0 and

1. Even though no new morphospace is generated, we have a difference of

1 for 25 of the 45 comparisons. Thus, the average pairwise dissimilarity

now increases to $\frac{25}{45}$=0.56. Similarly, we now have multiple opportunities to

observe the 4th state pairs (e.g., 00 and 01, and 10 and 11). So, even if

Character B changes only once (with either State 0 or State 1 diagnosing a

clade of 5 taxa), then it still will maximize the possible disparity for the

character and decrease the possible compatibility for the character simply

because of the phylogenetic distribution of the trait.

This relationship pertains only to an "existing" set of character states. The

introduction of novel states will increase both disparity and compatibility.

Consider a 3-state character:

     Character C: 0 0 0 0 0 1 1 1 1 2

The character is largely identical to Character B, but a "new" state evolved in

addition. This *increases* the probability of compatibility by decreasing the

opportunities for mismatch: there now are only 3 opportunities to pair State

1 with a second state from another character and there are zero

opportunities to pair State 2 with a second state from another character.

Moreover, we now have increased the disparity: 29 of the comparisons now

do not match, yielding a disparity of $\frac{29}{45} = 0.64$. This returns to the important

difference between rates of character change and rates of state derivation

described in the paper: when rates of state derivation are high relative to

rates of change, then both disparity and compatibility will be high. However,

as the rates drop, then disparity will increase (up to some limit) whereas

compatibility will drop.

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SUPPLEMENT B: RESULTS

1. RATES OF CHARACTER CHANGE

Best single rate, gamma and lognormal models for character rates. "S" gives taxon richness of a clade. "N_c" gives the number of characters. "δ" gives the average rate of change per taxon. "α" gives the shape (and scale) parameter of the best gamma distribution. "σ" gives the order of magnitude change in rates per standard deviation for the best lognormal distribution.

Clade	Taxon	Study	S	N_c	Single δ	Single $\ln L[\delta]$	Gamma δ	Gamma α	Gamma $\ln L[\delta,\alpha]$	Lognormal δ	Lognormal σ	Lognormal $\ln L[\delta,\sigma]$
Moll.	Cardiidae	Schneider 1998b	33	24	0.24	-89.8	0.24	0.78	-65.0	0.24	3.09	-64.6
Moll.	Cardiinae	Schneider 2002	23	22	0.21	-66.7	0.19	0.76	-54.1	0.21	2.87	-53.4
Moll.	*Chione*	Roopnarine 2001	19	22	0.28	-75.2	0.28	1.14	-58.6	0.28	2.68	-58.2
Moll.	*Chionopsis*	Roopnarine 2001	19	23	0.26	-79.1	0.23	0.80	-60.3	0.24	2.95	-60.4
Moll.	Corbulidae	Anderson & Roopnarine 2003	12	70	0.07	-179.3	0.07	1.10	-159.1	0.08	2.65	-159.4
Moll.	Eucardiidae	Schneider 1998a	20	16	0.45	-66.2	0.35	0.56	-44.3	0.35	3.69	-44.6
Moll.	Hippuritoidea	Stone & Telford 1999	14	12	0.26	-27.9	0.22	0.79	-24.4	0.23	3.14	-24.2
Moll.	Hippuritoidea	Skelton & Smith 2000	36	32	0.11	-94.7	0.11	0.50	-72.0	0.11	4.00	-70.7
Moll.	*Leptodesma*	Rode 2004	22	27	0.27	-100.1	0.27	1.12	-76.2	0.27	2.58	-76.2
Moll.	Ostreaoidea	Huelsenbeck 1994	37	34	0.13	-119.7	0.14	0.47	-84.6	0.15	4.16	-82.8
Moll.	Heteromorphs	Monks 1999	26	26	0.12	-68.8	0.11	0.45	-54.0	0.12	4.37	-52.6
Moll.	Ceratitida	McGowan & Smith 2007	32	55	0.11	-214.1	0.11	0.82	-151.9	0.12	3.01	-151.1
Moll.	Goniatoidea	Korn 1997	13	24	0.10	-50.6	0.07	0.47	-42.9	0.08	4.24	-42.0
Moll.	Hamitidae	Monks 2002	27	30	0.12	-90.5	0.11	0.37	-67.1	0.12	4.38	-65.5
Moll.	Hammatoceratinae	Neige & Dommergues 1995	12	16	0.33	-40.6	0.35	1.47	-36.7	0.37	2.40	-36.7
Moll.	Hildoceratidae	Rulleau *et al.* 2003	17	19	0.38	-60.0	0.39	1.65	-51.2	0.40	2.24	-51.4
Moll.	*Semiformiceras*	Cecca & Rouget 2006	11	14	0.35	-33.6	0.37	1.26	-30.7	0.39	2.50	-30.8
Moll.	Ancillinae	Michaux 1989	33	36	0.12	-132.9	0.12	0.31	-85.0	0.13	5.62	-82.7
Moll.	Bucaniidae	Wagner 2001	42	33	0.24	-151.5	0.25	0.96	-99.0	0.25	2.97	-98.8
Moll.	Columbellidae	de Maintenon 2005	24	30	0.21	-114.2	0.19	0.68	-81.2	0.20	3.19	-81.0
Moll.	Eotomariidae	Wagner 1999	41	69	0.11	-327.3	0.11	0.72	-203.7	0.11	3.31	-203.5
Moll.	Harpidae	Merle & Pacaud 2003	20	31	0.14	-95.4	0.13	0.62	-73.7	0.14	3.41	-72.9
Moll.	Macluritidae	Wagner 1999	18	50	0.11	-166.0	0.09	0.66	-126.7	0.10	3.19	-126.7
Moll.	Murchisoniidae	Wagner 1999	34	67	0.08	-253.0	0.08	0.63	-178.3	0.08	3.37	-177.0
Moll.	Nassariidae	Haasl 2000	35	25	0.30	-98.8	0.33	1.44	-73.5	0.32	2.50	-72.9

Clade	Taxon	Study	S	N_C	Single		Gamma			Lognormal		
					δ	$lnL[\delta]$	δ	α	$lnL[\delta,\alpha]$	δ	σ	$lnL[\delta,\sigma]$
Moll.	Oceanibrinae	Merle 2005	15	22	0.17	-57.4	0.14	0.61	-48.2	0.16	3.15	-47.6
Moll.	Rapaninae	Vermeij & Carlson 2000	45	34	0.32	-171.8	0.35	1.35	-111.7	0.34	2.51	-111.2
Moll.	Subulitoidea	Nützel *et al.* 2000	27	17	0.41	-63.4	0.41	1.17	-47.7	0.40	2.64	-47.7
Moll.	Trochonematoidea	Wagner 1995	55	43	0.21	-245.7	0.25	0.76	-137.4	0.25	3.32	-137.1
Moll.	Tropidodiscidae	Wagner 2001	22	33	0.17	-115.4	0.16	0.75	-86.4	0.17	3.04	-86.2
Moll.	Cyrtonellidae	Wagner 2001	22	30	0.18	-100.4	0.17	0.79	-77.2	0.18	2.88	-76.7
Moll.	Conocardioidea	Wagner 1997	43	53	0.11	-260.6	0.10	0.48	-163.3	0.10	4.05	-164.8
Moll.	Pseudobigaleaidae	Wagner 1997	24	62	0.09	-231.5	0.07	0.43	-157.9	0.08	4.14	-157.1
Moll.	Eopteriidae	Wagner 1997	20	44	0.12	-159.4	0.11	0.53	-113.0	0.11	3.61	-112.5
Moll.	Ribeiriidae	Wagner 1997	27	34	0.23	-129.4	0.23	1.42	-97.6	0.23	2.47	-97.4
Moll.	Technophoridae	Wagner 1997	14	40	0.11	-108.4	0.09	0.76	-92.1	0.10	2.91	-92.1
Moll.	Leptochitonidae	Sigwart *et al.* 2006	21	43	0.19	-157.0	0.20	1.57	-124.7	0.20	2.30	-125.0
Moll.	Paleoloricata	Cherns 2004	30	27	0.32	-114.5	0.30	0.99	-80.3	0.30	2.73	-81.0
Trilo.	Agnostoidea	Westrop *et al.* 1996	43	28	0.34	-132.8	0.36	1.06	-89.4	0.37	2.70	-89.3
Trilo.	Alokistocaridae	Sundberg 1999	19	50	0.14	-176.7	0.14	1.08	-137.4	0.14	2.65	-138.3
Trilo.	Basal Trilobites	Lieberman 2002	17	29	0.25	-94.8	0.27	1.44	-78.1	0.28	2.42	-78.4
Trilo.	Bristoliinae	Lieberman 1999	11	17	0.23	-39.6	0.20	0.79	-35.7	0.22	2.80	-35.7
Trilo.	Burlingiidae	Ebbestad & Budd 2001	16	18	0.31	-58.4	0.26	0.57	-45.0	0.29	3.26	-45.0
Trilo.	Dokimocephalidae	Westrop *et al.* 2010	25	23	0.28	-93.9	0.22	0.43	-61.6	0.24	4.05	-61.5
Trilo.	Emuellids	Paterson & Edgecombe 2006	27	45	0.14	-166.4	0.14	0.95	-123.4	0.14	2.79	-122.8
Trilo.	Euptychaspidines	Adrain & Westrop 2001	12	25	0.14	-58.1	0.12	0.79	-52.1	0.13	2.93	-51.8
Trilo.	Holmiids	Lieberman 1999	18	35	0.17	-114.6	0.17	1.19	-91.9	0.17	2.61	-91.5
Trilo.	Iwayaspidines	Hughes & Rushton 1990	14	23	0.25	-65.0	0.27	1.38	-56.6	0.27	2.47	-56.7
Trilo.	Kochaspids	Sundberg 2004	66	70	0.25	-487.3	0.26	1.28	-264.0	0.25	2.52	-267.7
Trilo.	Olenellina	Lieberman 2001	26	57	0.16	-201.6	0.17	2.10	-166.7	0.17	2.08	-166.9
Trilo.	Olenelloids	Lieberman 1998	26	79	0.11	-270.9	0.12	2.40	-229.4	0.12	1.98	-229.3
Trilo.	*Olenellus*	Lieberman 1999	12	13	0.40	-32.9	0.43	1.52	-29.8	0.45	2.40	-29.9
Trilo.	Oryctocephalids	Sundberg & McCollum 1997	22	36	0.21	-132.3	0.21	1.36	-102.0	0.21	2.46	-101.9
Trilo.	Oryctocephalines	Sundberg 2006	24	20	0.38	-74.8	0.38	1.24	-57.0	0.38	2.53	-57.2
Trilo.	Polymeroids	Babcock 1994	19	26	0.18	-77.0	0.16	0.87	-63.0	0.17	2.79	-62.7
Trilo.	Ptychyoparioids	Cotton 2001	49	72	0.10	-335.9	0.11	0.72	-214.7	0.12	3.22	-213.1
Trilo.	Wuaniids	Bentley & Jago 2004	38	14	0.88	-60.7	0.94	2.23	-45.3	0.92	2.04	-45.2

Clade	Taxon	Study	S	N_C	Single		Gamma			Lognormal		
					δ	lnL[δ]	δ	α	lnL[δ,α]	δ	σ	lnL[δ,σ]
Trilo.	Acanthoparyphines	Adrain 1998	24	39	0.11	-127.1	0.10	0.49	-92.8	0.11	4.00	-91.5
Trilo.	*Ceratocara*	Chatterton *et al.* 1997	10	29	0.13	-66.6	0.08	0.27	-57.1	0.10	4.97	-57.1
Trilo.	Deiphonines	Congreve & Lieberman 2010	21	27	0.27	-104.6	0.25	0.86	-75.5	0.25	2.91	-75.7
Trilo.	Dimeropygids	Adrain *et al.* 2001	18	25	0.20	-84.0	0.19	0.53	-61.8	0.21	3.65	-61.0
Trilo.	Illaenids	Amati & Westrop 2004	28	20	0.38	-72.0	0.40	1.71	-57.4	0.40	2.28	-57.1
Trilo.	*Ovalocephalus*	Zhiyi *et al.* 2010	10	17	0.20	-34.5	0.20	2.65	-33.5	0.20	1.96	-33.4
Trilo.	*Pseudopetigurus*	Wenwei *et al.* 2006	17	25	0.26	-81.6	0.26	1.12	-66.1	0.26	2.60	-66.4
Trilo.	Reedocalymenines	Turvey 2002	32	25	0.27	-100.4	0.30	1.02	-71.0	0.30	2.87	-69.7
Trilo.	Shumardiids	Waisfeld *et al.* 2001	33	52	0.19	-196.3	0.20	2.40	-159.5	0.20	1.98	-159.2
Trilo.	*Stenoblepharum*	Edgecombe *et al.* 1997	10	18	0.22	-38.2	0.22	2.20	-36.6	0.23	2.05	-36.6
Trilo.	Tetralichines	Carlucci *et al.* 2010	14	25	0.17	-63.0	0.17	1.71	-57.0	0.17	2.38	-56.6
Trilo.	Toernquistids	Chatterton *et al.* 1998	38	55	0.16	-252.7	0.17	1.09	-169.3	0.16	2.71	-169.4
Trilo.	Acanthopyge	Ebach & Ahyong 2001	25	15	0.62	-55.8	0.67	1.73	-43.8	0.67	2.28	-43.9
Trilo.	*Edgecombaspis*	Adrain & Ramsköld 1997	9	16	0.19	-31.9	0.13	0.47	-29.4	0.17	3.44	-29.4
Trilo.	Encrinurines	Adrain & Edgecombe 1997	32	40	0.13	-146.7	0.12	0.59	-104.0	0.13	3.54	-102.9
Trilo.	Odontopleurids	Ramsköld & Chatterton 1991	62	35	0.34	-223.0	0.38	0.87	-120.5	0.38	3.08	-122.5
Trilo.	Phacopids	Ramsköld & Werdelin 1991	47	32	0.50	-173.7	0.49	1.52	-114.2	0.47	2.26	-115.6
Trilo.	Trochurines	Campbell & Chatterton 2007	19	21	0.36	-70.9	0.38	1.71	-58.5	0.38	2.24	-58.5
Trilo.	Asteropygines	Lieberman & Kloc 1997	38	66	0.16	-296.2	0.16	1.54	-212.6	0.16	2.28	-213.3
Trilo.	*Basidechenella*	Lieberman 1994	16	25	0.23	-81.0	0.20	0.66	-62.8	0.21	3.22	-63.2
Trilo.	Calmoniids	Lieberman *et al.* 1991	14	51	0.10	-145.7	0.09	0.73	-121.3	0.10	2.97	-121.0
Trilo.	Calmoniids	Lieberman 1993	17	38	0.14	-117.1	0.13	1.04	-95.0	0.14	2.74	-94.2
Trilo.	*Dechenella*	Lieberman 1994	18	47	0.14	-152.8	0.14	1.22	-124.7	0.14	2.54	-125.2
Trilo.	Koneprusiines	Adrain *et al.* 2008	39	23	0.52	-114.5	0.54	1.50	-75.6	0.52	2.40	-75.8
Trilo.	Proetids	Lieberman 1994	21	52	0.10	-175.0	0.10	0.73	-134.5	0.11	2.88	-133.1
Trilo.	*Trimerocephalus*	Crônier 2003	14	23	0.15	-59.7	0.11	0.39	-47.6	0.12	4.38	-46.9
Trilo.	Phillipsids	Brezinski 2003, 2005	21	25	0.31	-97.5	0.32	1.08	-71.0	0.32	2.78	-71.2
Trilo.	Lichoidea	Pollitt *et al.* 2005	36	48	0.20	-215.3	0.21	1.46	-150.1	0.21	2.44	-149.7
Echino.	Arbacoids	Smith & Wright 1993	22	40	0.07	-102.2	0.07	0.50	-81.4	0.08	4.37	-79.0
Echino.	Arbacoids	Smith 1994	26	26	0.26	-93.9	0.25	1.15	-71.7	0.25	2.63	-71.8
Echino.	Cassiduloids	Saucede & Neraudeau 2006	51	31	0.25	-162.2	0.29	0.60	-94.0	0.30	3.56	-93.1
Echino.	Disasteroids	Barras 2007	26	19	0.25	-59.0	0.22	0.74	-47.2	0.25	2.88	-46.7

Clade	Taxon	Study	S	N_C	Single δ	lnL[δ]	Gamma δ	α	lnL[δ,α]	Lognormal δ	σ	lnL[δ,σ]
Echino.	Holasteroids	Smith 2004	43	34	0.19	-147.2	0.21	0.56	-96.7	0.23	3.54	-95.1
Echino.	Irregularia	Saucède et al. 2007	33	39	0.19	-179.8	0.18	0.64	-111.6	0.17	3.62	-111.6
Echino.	Loveniids	Kroh 2007	32	42	0.20	-178.0	0.21	1.33	-125.5	0.20	2.56	-125.0
Echino.	Irregularia	Smith 2007	46	54	0.10	-236.5	0.12	0.47	-147.4	0.12	4.29	-144.3
Echino.	Early Echinoids	Smith & Savill 2001	11	27	0.15	-63.3	0.12	0.72	-56.8	0.14	2.89	-56.8
Echino.	Somaliasterids	Jeffery 1999	19	24	0.21	-80.0	0.17	0.51	-59.0	0.19	3.73	-58.6
Echino.	Spatongoids	Villier et al. 2004	36	35	0.24	-152.8	0.24	1.16	-106.4	0.24	2.63	-106.7
Echino.	Spatangoids	Cunningham & Jeffery Abt 2009	37	42	0.18	-163.0	0.19	1.40	-124.6	0.19	2.38	-124.2
Echino.	Temnopleurids	Jeffery & Emlet 2003	17	38	0.12	-123.4	0.09	0.36	-89.0	0.10	4.64	-88.1
Echino.	Agelacrinitines	Smith & Arbizu 1987	13	12	0.37	-32.8	0.29	0.45	-27.0	0.34	3.62	-27.0
Echino.	Edrioasteroids	Sumrall et al. 2006	15	24	0.15	-64.3	0.12	0.49	-51.9	0.13	4.00	-51.3
Echino.	Glyptocystitids	Sumrall & Brett 2002	11	19	0.22	-45.2	0.21	1.00	-40.8	0.23	2.70	-40.8
Echino.	Pleurocystitid	Sumrall & Sprinkle 1995	12	23	0.16	-55.6	0.12	0.57	-48.1	0.14	3.37	-47.8
Echino.	Basal_Crinoids	Ausich 1998a	33	25	0.45	-91.4	0.46	3.08	-76.9	0.46	1.81	-76.9
Echino.	Botryocrinids	Gahn & Kammer 2002	13	14	0.35	-37.2	0.35	1.22	-32.7	0.36	2.54	-32.7
Echino.	Calceocrinids	Harvey & Ausich 1997	22	17	0.44	-58.6	0.45	1.71	-48.0	0.46	2.23	-48.0
Echino.	Camerates	Ausich 1998b	28	27	0.29	-99.6	0.28	1.53	-77.9	0.28	2.33	-78.0
Echino.	Cladids	Ausich 1998b	27	21	0.27	-68.7	0.25	1.14	-55.2	0.25	2.57	-55.4
Echino.	Cyathocrinites	Kammer & Gahn 2003	14	14	0.36	-40.1	0.31	0.70	-33.3	0.34	2.98	-33.4
Echino.	Flexibilia	Brower 2001	13	19	0.25	-48.1	0.24	1.61	-43.9	0.25	2.24	-43.9
Echino.	Anomalocystitids	Ruta 1999	20	97	0.05	-346.3	0.05	0.54	-247.8	0.05	3.69	-245.6
Echino.	Cinctans	Smith & Wright 2003	21	57	0.08	-183.0	0.07	0.58	-138.3	0.08	3.41	-136.7
Echino.	Chauvelicystines	Lee et al. 2005	12	15	0.32	-38.2	0.32	1.23	-33.9	0.34	2.63	-33.8
Echino.	Cornutes	Cripps 1991	32	72	0.06	-251.7	0.07	0.47	-177.5	0.07	4.37	-173.8
Echino.	Cornutes	Lefebvre 2001	28	18	0.35	-66.4	0.34	0.91	-49.2	0.35	2.88	-49.2
Echino.	Mitrates	Parsley 1997	42	42	0.13	-169.4	0.12	0.41	-110.6	0.13	4.00	-108.5

2. RATES OF STATE DERIVATION

Best single rate, gamma and lognormal models for state derivation rates. "S" gives taxon richness of a clade. "N_S" gives the number of derived states. "δ" gives the average rate of state derivation per sampled taxon. "α" gives the shape (and scale) parameter of the best gamma distribution. "σ" gives the order of magnitude change in rates per standard deviation for the best lognormal distribution.

Clade	Taxon	Study	S	N_S	Single δ	Single lnL[δ]	Gamma δ	Gamma α	Gamma lnL[δ,α]	Lognormal δ	Lognormal σ	Lognormal lnL[δ,σ]
Moll.	Cardiids	Schneider 1998b	33	45	0.09	-89.8	0.06	0.67	-65.0	0.07	3.41	-64.6
Moll.	Cardiines	Schneider 2002	23	46	0.08	-66.7	0.04	0.62	-54.1	0.04	4.00	-53.4
Moll.	Chione	Roopnarine 2001	19	30	0.24	-75.2	0.14	1.29	-58.6	0.15	2.38	-58.2
Moll.	Chionopsis	Roopnarine 2001	19	35	0.20	-79.1	0.09	0.83	-60.3	0.10	2.96	-60.4
Moll.	Corbulids	Anderson & Roopnarine 2003	12	125	0.22	-179.3	0.02	1.65	-159.1	0.02	2.17	-159.4
Moll.	Eucardiids	Schneider 1998a	20	36	0.15	-66.2	0.08	0.50	-44.3	0.09	4.37	-44.6
Moll.	Hippuritoids	Stone & Telford 1999	14	15	0.17	-27.9	0.12	0.57	-24.4	0.13	3.73	-24.2
Moll.	Hippuritoids	Skelton & Smith 2000	36	36	0.09	-94.7	0.07	0.62	-72.0	0.07	3.62	-70.7
Moll.	Leptodesma	Rode 2004	22	31	0.29	-100.1	0.20	0.94	-76.2	0.20	2.81	-76.2
Moll.	Ostreaoids	Huelsenbeck 1994	37	41	0.10	-119.7	0.09	0.76	-84.6	0.10	3.37	-82.8
Moll.	Heteromorphs	Monks 1999	26	29	0.10	-68.8	0.08	0.75	-54.0	0.08	3.27	-52.6
Moll.	Ceratitida	McGowan & Smith 2007	32	77	0.14	-214.1	0.06	0.95	-151.9	0.06	2.87	-151.1
Moll.	Goniatoids	Korn 1997	13	24	0.18	-50.6	0.07	0.47	-42.9	0.08	4.24	-42.0
Moll.	Hamitids	Monks 2002	27	43	0.09	-90.5	0.04	0.54	-67.1	0.05	4.24	-65.5
Moll.	Hammatoceratines	Neige & Dommergues 1995	12	20	0.34	-40.6	0.20	1.78	-36.7	0.20	2.13	-36.7
Moll.	Hildoceratids	Rulleau et al. 2003	17	27	0.29	-60.0	0.18	1.53	-51.2	0.18	2.28	-51.4
Moll.	Semiformiceras	Cecca & Rouget 2006	11	25	0.22	-33.6	0.08	1.26	-30.7	0.08	2.38	-30.8
Moll.	Ancillines	Michaux 1989	33	36	0.13	-132.9	0.12	0.31	-85.0	0.13	5.62	-82.7
Moll.	Bucaniids	Wagner 2001	42	61	0.10	-151.5	0.07	1.15	-99.0	0.07	2.63	-98.8
Moll.	Columbellids	de Maintenon 2005	24	43	0.19	-114.2	0.09	1.10	-81.2	0.10	2.58	-81.0
Moll.	Eotomariids	Wagner 1999	41	137	0.09	-327.3	0.03	2.16	-203.7	0.03	1.99	-203.5
Moll.	Harpids	Merle & Pacaud 2003	20	58	0.10	-95.4	0.03	0.67	-73.7	0.03	3.58	-72.9
Moll.	Macluritids	Wagner 1999	18	84	0.17	-166.0	0.03	0.62	-126.7	0.03	3.69	-126.7
Moll.	Murchisoniids	Wagner 1999	34	122	0.09	-253.0	0.02	1.22	-178.3	0.02	2.45	-177.0
Moll.	Nassariids	Haasl 2000	35	37	0.14	-98.8	0.14	1.42	-73.5	0.14	2.38	-72.9
Moll.	Oceanibrines	Merle 2005	15	37	0.13	-57.4	0.03	0.62	-48.2	0.04	3.69	-47.6

Clade	Taxon	Study	S	N_S	Single		Gamma			Lognormal		
					δ	$lnL[\delta]$	δ	α	$lnL[\delta,\alpha]$	δ	σ	$lnL[\delta,\sigma]$
Moll.	Rapanines	Vermeij & Carlson 2000	45	48	0.17	-171.8	0.18	1.21	-111.7	0.18	2.61	-111.2
Moll.	Subulitoids	Nützel et al. 2000	27	28	0.15	-63.4	0.14	0.57	-47.7	0.15	3.65	-47.7
Moll.	Trochonematoids	Wagner 1995	55	64	0.11	-245.7	0.10	1.26	-137.4	0.10	2.50	-137.1
Moll.	Tropidodiscids	Wagner 2001	22	57	0.14	-115.4	0.05	1.02	-86.4	0.05	2.87	-86.2
Moll.	Cyrtonellids	Wagner 2001	22	48	0.15	-100.4	0.06	0.57	-77.2	0.06	3.73	-76.7
Moll.	Conocardioids	Wagner 1997	43	87	0.12	-260.6	0.07	0.87	-163.3	0.07	3.14	-164.8
Moll.	Pseudobigaleaids	Wagner 1997	24	61	0.16	-231.5	0.06	0.87	-157.9	0.06	3.08	-157.1
Moll.	Eopteriids	Wagner 1997	20	84	0.21	-159.4	0.05	0.83	-113.0	0.05	3.02	-112.5
Moll.	Ribeiriids	Wagner 1997	27	56	0.15	-129.4	0.06	0.84	-97.6	0.06	2.78	-97.4
Moll.	Technophorids	Wagner 1997	14	101	0.23	-108.4	0.03	1.10	-92.1	0.03	2.52	-92.1
Moll.	Leptochitonids	Sigwart et al. 2006	21	68	0.18	-157.0	0.05	1.32	-124.7	0.06	2.50	-125.0
Moll.	Paleoloricates	Cherns 2004	30	61	0.09	-114.5	0.03	0.64	-80.3	0.04	3.34	-81.0
Trilo.	Agnostoids	Westrop et al. 1996	43	43	0.14	-132.8	0.15	0.87	-89.4	0.16	2.97	-89.3
Trilo.	Alokistocarids	Sundberg 1999	19	101	0.18	-176.7	0.03	1.26	-137.4	0.03	2.40	-138.3
Trilo.	Basal Trilobites	Lieberman 2002	17	40	0.31	-94.8	0.13	1.67	-78.1	0.13	2.25	-78.4
Trilo.	Bristoliines	Lieberman 1999	11	23	0.25	-39.6	0.08	0.47	-35.7	0.09	4.04	-35.7
Trilo.	Burlingiids	Ebbestad & Budd 2001	16	18	0.35	-58.4	0.26	0.57	-45.0	0.29	3.26	-45.0
Trilo.	Dokimocephalids	Westrop et al. 2010	25	32	0.19	-93.9	0.12	0.45	-61.6	0.12	4.25	-61.5
Trilo.	Emuellids	Paterson & Edgecombe 2006	27	53	0.20	-166.4	0.09	0.59	-123.4	0.10	3.41	-122.8
Trilo.	Euptychaspidines	Adrain & Westrop 2001	12	33	0.21	-58.1	0.06	0.68	-52.1	0.06	3.37	-51.8
Trilo.	Holmiids	Lieberman 1999	18	44	0.27	-114.6	0.09	0.57	-91.9	0.10	3.46	-91.5
Trilo.	Iwayaspidines	Hughes & Rushton 1990	14	30	0.31	-65.0	0.13	1.24	-56.6	0.14	2.47	-56.7
Trilo.	Kochaspids	Sundberg 2004	66	149	0.12	-487.3	0.07	1.36	-264.0	0.07	2.55	-267.7
Trilo.	Olenellina	Lieberman 2001	26	84	0.24	-201.6	0.08	1.49	-166.7	0.08	2.38	-166.9
Trilo.	Olenelloids	Lieberman 1998	26	136	0.20	-270.9	0.04	1.67	-229.4	0.04	2.28	-229.3
Trilo.	Olenellus	Lieberman 1999	12	16	0.34	-32.9	0.25	1.75	-29.8	0.26	2.24	-29.9
Trilo.	Oryctocephalids	Sundberg & McCollum 1997	22	76	0.16	-132.3	0.04	1.98	-102.0	0.04	2.05	-101.9
Trilo.	Oryctocephalines	Sundberg 2006	24	42	0.15	-74.8	0.08	1.24	-57.0	0.08	2.50	-57.2
Trilo.	Polymeroids	Babcock 1994	19	41	0.14	-77.0	0.05	0.73	-63.0	0.06	3.15	-62.7
Trilo.	Ptychyoparioids	Cotton 2001	49	113	0.09	-335.9	0.04	0.95	-214.7	0.04	2.87	-213.1
Trilo.	Wuaniids	Bentley & Jago 2004	38	25	0.18	-60.7	0.30	1.77	-45.3	0.30	2.28	-45.2
Trilo.	Acanthoparyphines	Adrain 1998	24	50	0.14	-127.1	0.06	0.49	-92.8	0.06	4.00	-91.5

Clade	Taxon	Study	S	N_S	Single δ	$\ln L[\delta]$	Gamma δ	α	$\ln L[\delta,\alpha]$	Lognormal δ	σ	$\ln L[\delta,\sigma]$
Trilo.	Ceratocara	Chatterton et al. 1997	10	30	0.35	-66.6	0.07	0.25	-57.1	0.09	5.28	-57.1
Trilo.	Deiphonines	Congreve & Lieberman 2010	21	29	0.32	-104.6	0.22	0.94	-75.5	0.23	2.79	-75.7
Trilo.	Dimeropygids	Adrain et al. 2001	18	35	0.20	-84.0	0.07	0.56	-61.8	0.08	3.69	-61.0
Trilo.	Illaenids	Amati & Westrop 2004	28	40	0.13	-72.0	0.08	0.98	-57.4	0.09	2.82	-57.1
Trilo.	Ovalocephalus	Zhiyi et al. 2010	10	28	0.18	-34.5	0.04	0.70	-33.5	0.04	3.44	-33.4
Trilo.	Pseudopetigurus	Wenwei et al. 2006	17	40	0.24	-81.6	0.09	1.10	-66.1	0.09	2.57	-66.4
Trilo.	Reedocalymenines	Turvey 2002	32	33	0.16	-100.4	0.17	0.70	-71.0	0.18	3.37	-69.7
Trilo.	Shumardiids	Waisfeld et al. 2001	33	99	0.16	-196.3	0.05	2.17	-159.5	0.05	2.04	-159.2
Trilo.	Stenoblepharum	Edgecombe et al. 1997	10	26	0.25	-38.2	0.08	1.12	-36.6	0.08	2.40	-36.6
Trilo.	Tetralichines	Carlucci et al. 2010	14	39	0.18	-63.0	0.05	0.57	-57.0	0.05	3.69	-56.6
Trilo.	Toernquistids	Chatterton et al. 1998	38	85	0.15	-252.7	0.07	1.14	-169.3	0.07	2.63	-169.4
Trilo.	Acanthopyge	Ebach & Ahyong 2001	25	23	0.24	-55.8	0.26	1.10	-43.8	0.26	2.66	-43.9
Trilo.	Edgecombaspis	Adrain & Ramsköld 1997	9	19	0.27	-31.9	0.09	0.53	-29.4	0.10	3.69	-29.4
Trilo.	Encrinurines	Adrain & Edgecombe 1997	32	56	0.12	-146.7	0.06	1.04	-104.0	0.06	2.63	-102.9
Trilo.	Odontopleurids	Ramsköld & Chatterton 1991	62	57	0.12	-223.0	0.16	0.80	-120.5	0.16	3.18	-122.5
Trilo.	Phacopids	Ramsköld & Werdelin 1991	47	88	0.12	-173.7	0.07	2.37	-114.2	0.07	1.95	-115.6
Trilo.	Trochurines	Campbell & Chatterton 2007	19	37	0.22	-70.9	0.10	1.66	-58.5	0.11	2.15	-58.5
Trilo.	Asteropygines	Lieberman & Kloc 1997	38	104	0.18	-296.2	0.07	0.95	-212.6	0.07	2.86	-213.3
Trilo.	Basidechenella	Lieberman 1994	16	32	0.28	-81.0	0.11	0.62	-62.8	0.12	3.26	-63.2
Trilo.	Calmoniids	Lieberman et al. 1991	14	61	0.30	-145.7	0.05	0.52	-121.3	0.06	3.58	-121.0
Trilo.	Calmoniids	Lieberman 1993	17	48	0.24	-117.1	0.07	0.54	-95.0	0.08	3.73	-94.2
Trilo.	Dechenella	Lieberman 1994	18	68	0.25	-152.8	0.06	0.91	-124.7	0.06	2.79	-125.2
Trilo.	Koneprusiines	Adrain et al. 2008	39	32	0.22	-114.5	0.29	1.80	-75.6	0.29	2.21	-75.8
Trilo.	Proetids	Lieberman 1994	21	58	0.23	-175.0	0.08	0.66	-134.5	0.09	3.37	-133.1
Trilo.	Trimerocephalus	Crônier 2003	14	33	0.16	-59.7	0.05	0.62	-47.6	0.05	3.55	-46.9
Trilo.	Phillipsids	Brezinski 2003, 2005	21	30	0.30	-97.5	0.22	1.16	-71.0	0.22	2.62	-71.2
Trilo.	Lichoidea	Pollitt et al. 2005	36	89	0.14	-215.3	0.06	0.62	-150.1	0.07	3.51	-149.7
Echino.	Arbacoids	Smith & Wright 1993	22	48	0.10	-102.2	0.04	0.50	-81.4	0.05	4.38	-79.0
Echino.	Arbacoids	Smith 1994	26	41	0.16	-93.9	0.09	1.41	-71.7	0.10	2.30	-71.8
Echino.	Cassiduloids	Saucede & Neraudeau 2006	51	47	0.10	-162.2	0.10	0.90	-94.0	0.10	2.88	-93.1
Echino.	Disasteroids	Barras 2007	26	28	0.12	-59.0	0.10	0.95	-47.2	0.11	2.87	-46.7
Echino.	Holasteroids	Smith 2004	43	51	0.10	-147.2	0.08	0.76	-96.7	0.08	3.14	-95.1

Clade	Taxon	Study	S	N_S	Single δ	lnL[δ]	Gamma δ	α	lnL[δ,α]	Lognormal δ	σ	lnL[δ,σ]
Echino.	Irregularia	Saucède et al. 2007	33	59	0.15	-179.8	0.08	0.79	-111.6	0.09	3.13	-111.6
Echino.	Loveniids	Kroh 2007	32	75	0.14	-178.0	0.06	1.51	-125.5	0.06	2.28	-125.0
Echino.	Irregularia	Smith 2007	46	77	0.08	-236.5	0.05	0.43	-147.4	0.06	4.46	-144.3
Echino.	Early Echinoids	Smith & Savill 2001	11	32	0.27	-63.3	0.07	0.74	-56.8	0.08	2.90	-56.8
Echino.	Somaliasterids	Jeffery 1999	19	31	0.20	-80.0	0.10	0.49	-59.0	0.11	3.88	-58.6
Echino.	Spatongoids	Villier et al. 2004	36	63	0.13	-152.8	0.07	2.19	-106.4	0.07	1.98	-106.7
Echino.	Spatangoids	Cunningham & Jeffery Abt 2009	37	68	0.13	-163.0	0.07	1.56	-124.6	0.07	2.28	-124.2
Echino.	Temnopleurids	Jeffery & Emlet 2003	17	49	0.21	-123.4	0.05	0.51	-89.0	0.06	3.88	-88.1
Echino.	Agelacrinitines	Smith & Arbizu 1987	13	16	0.25	-32.8	0.17	0.92	-27.0	0.18	2.71	-27.0
Echino.	Edrioasteroids	Sumrall et al. 2006	15	27	0.21	-64.3	0.10	0.46	-51.9	0.11	4.00	-51.3
Echino.	Glyptocystitids	Sumrall & Brett 2002	11	24	0.29	-45.2	0.10	0.55	-40.8	0.11	3.37	-40.8
Echino.	Pleurocystitid	Sumrall & Sprinkle 1995	12	26	0.26	-55.6	0.10	0.65	-48.1	0.11	3.24	-47.8
Echino.	Basal_Crinoids	Ausich 1998a	33	69	0.12	-91.4	0.05	2.05	-76.9	0.05	2.04	-76.9
Echino.	Botryocrinids	Gahn & Kammer 2002	13	21	0.24	-37.2	0.13	2.01	-32.7	0.14	2.00	-32.7
Echino.	Calceocrinids	Harvey & Ausich 1997	22	32	0.18	-58.6	0.11	0.80	-48.0	0.12	3.08	-48.0
Echino.	Camerates	Ausich 1998b	28	72	0.10	-99.6	0.03	0.70	-77.9	0.04	3.41	-78.0
Echino.	Cladids	Ausich 1998b	27	46	0.09	-68.7	0.04	0.90	-55.2	0.04	3.05	-55.4
Echino.	Cyathocrinites	Kammer & Gahn 2003	14	17	0.29	-40.1	0.19	0.72	-33.3	0.21	3.03	-33.4
Echino.	Flexibilia	Brower 2001	13	34	0.18	-48.1	0.05	0.70	-43.9	0.05	3.44	-43.9
Echino.	Anomalocystitids	Ruta 1999	20	97	0.27	-346.3	0.05	0.54	-247.8	0.05	3.69	-245.6
Echino.	Cinctans	Smith & Wright 2003	21	80	0.15	-183.0	0.03	0.65	-138.3	0.04	3.58	-136.7
Echino.	Chauvelicystines	Lee et al. 2005	12	23	0.24	-38.2	0.11	1.91	-33.9	0.12	2.05	-33.8
Echino.	Cornutes	Cripps 1991	32	78	0.13	-251.7	0.05	0.66	-177.5	0.06	3.51	-173.8
Echino.	Cornutes	Lefebvre 2001	28	36	0.11	-66.4	0.07	1.06	-49.2	0.08	2.63	-49.2
Echino.	Mitrates	Parsley 1997	42	91	0.06	-169.4	0.02	1.12	-110.6	0.02	2.55	-108.5

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