

## Is It Better to Add Taxa or Characters to a Difficult Phylogenetic Problem?

ANNA GRAYBEAL<sup>1</sup>

*Department of Zoology, University of Texas, Austin, Texas 78712, USA*

**Abstract.**—The effects on phylogenetic accuracy of adding characters and/or taxa were explored using data generated by computer simulation. The conditions of this study were constrained but allowed for systematic investigation of certain parameters. The starting point for the study was a four-taxon tree in the “Felsenstein zone,” representing a difficult phylogenetic problem with an extreme situation of long branch attraction. Taxa were added sequentially to this tree in a manner specifically designed to break up the long branches, and for each tree data matrices of different sizes were simulated. Phylogenetic trees were reconstructed from these data using the criteria of parsimony and maximum likelihood. Phylogenetic accuracy was measured in three ways: (1) proportion of trees that are completely correct, (2) proportion of correctly reconstructed branches in all trees, and (3) proportion of trees in which the original four-taxon statement is correctly reconstructed. Accuracy improved dramatically with the addition of taxa and much more slowly with the addition of characters. If taxa can be added to break up long branches, it is much more preferable to add taxa than characters. [Long branch attraction; parsimony; phylogenetic reconstruction; simulation; taxon sampling.]

It is obvious that the successful reconstruction of phylogenetic relationships requires some amount of data sampling from relevant taxa and informative characters. Far less clear, however, is how much of each data type is required, and whether one of those sources of data has a greater impact on accuracy than the other. Given limited time and resources, it is important to explore the costs and benefits to phylogenetic accuracy of adding taxa versus increasing the number of characters. For example, given that one has sufficient time and resources to sequence 10 kilobases (kb) of DNA, would it be better to sequence, say, 2.5 kb from each of 4 taxa, or 1 kb from each of 10, or 0.25 kb from each of 40?

It is known that for some trees certain phylogenetic methods fail even with infinite data. This problem, called statistical inconsistency, was first demonstrated for parsimony and compatibility by Felsenstein (1978) for a four-taxon tree with unequal branch lengths (or rates of evolution). Subsequent workers found inconsistent branches

even in ultrametric trees (with unequal branch lengths) and in trees with five taxa (Hendy and Penny, 1989; DeBry, 1992; Zharkikh and Li, 1993). Steel (1989), Hendy and Charleston (1993), and Kim (1996) have also found inconsistent branches in large trees.

Hendy and Penny (1989) suggested that consistency problems could be alleviated by adding taxa to break up long branches, or, in other words, shortening the average branch length. Support for this idea comes from several paleontological studies (Gauthier et al., 1988; Donoghue et al., 1989; Huelsenbeck, 1991), all of which indicate that taxa that break up long branches within the ingroup (because they exhibit relatively primitive character states) have the strongest impact on phylogenetic conclusions. It is of interest to explore systematically how many taxa must be added (and where in the tree and with what branch lengths) for inconsistency or long-branch attraction problems to disappear. Kim (1996) conducted simulations to show that the addition of taxa does not necessarily alleviate inconsistency, but for the most part his added taxa did not break up long branches because he kept the average branch length constant. It remains to be seen how many taxa are needed to eliminate inconsistent branches if taxa are add-

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<sup>1</sup> Present address: Department of Zoology, Field Museum of Natural History, Roosevelt Road and Lake Shore Drive, Chicago, Illinois 60605, USA. E-mail: graybeal@fmppr.fmnh.org.

ed specifically to break up the long branches and thus reduce average branch length.

Another question concerns the relationship between adding taxa and adding characters in situations where inconsistency is not a problem (perhaps because enough taxa have been added to break up any long branches). In such situations one might think that phylogenetic accuracy will best be obtained by increasing the number of characters per taxon, rather than by adding even more taxa. This seems to be the commonly held view among systematists, among whom there is much attention focused on increasing the number of characters to resolve phylogenetic problems (e.g., Lecointre et al., 1993, 1994; Hillis et al., 1994; Cummings et al., 1995). There has not been extensive exploration of the effect on phylogenetic accuracy of adding both characters and taxa, and given that there may be a trade-off between these two data types it is of interest to explore this situation.

Simulation studies are a powerful tool for investigating the behavior of phylogenetic reconstruction over a range of precisely manipulated conditions (e.g., Nei, 1991; Huelsenbeck and Hillis, 1993; Kuhner and Felsenstein, 1994). This paper explores the effects of adding both taxa and characters on phylogenetic accuracy. The basic premise is to start with a difficult phylogenetic problem: data derived from a four-taxon tree in the "Felsenstein zone" known to be inconsistent for parsimony and other phylogenetic reconstruction methods. To examine the effect of adding taxa, the total amount of sequence data was held constant and taxa were added successively; thus in all resulting graphs the number of characters per taxon decreases as the number of taxa increases (e.g., if the total number of characters was 40,000, then for 4 taxa each taxon had 10,000 characters while for 30 taxa each taxon had 1,333 characters). To examine the effect of adding characters, this procedure was repeated for a range of character matrix sizes.

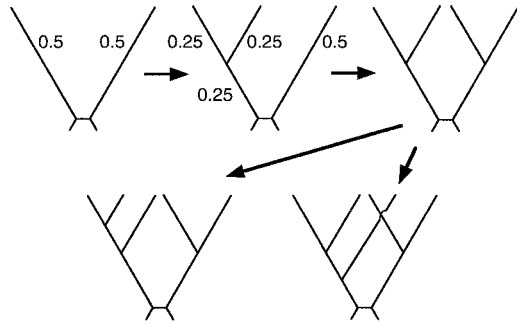


FIGURE 1. The four-taxon starting tree in the "Felsenstein zone," upper left, with demonstration of the taxon addition procedure implemented in this study: the single five-taxon and six-taxon trees and the two seven-taxon trees, one of which has the seventh branch added at the tip (lower left) and the other of which has it added at the base (lower right). Branch lengths are drawn proportional to the expected numbers of change: The starting four-taxon tree has two long branches of length 0.5 and three short branches of length 0.25. The larger trees maintain the three short branches at length 0.05, but the longer branches are divided into successively shorter and shorter ones as illustrated.

#### MATERIALS AND METHODS

Simulations were performed using the program Siminator, written in C by John Huelsenbeck and modified slightly by me. One hundred replicate data matrices of a given sequence length were simulated over each tree, with a kappa value (the ratio of transition rate, alpha, to transversion rate, beta) of 2 and rate variation determined by a gamma shape parameter of 0.5. Trees were reconstructed from the resulting datafiles using PAUP\* 4.0 (various developmental versions) (Swofford, unpubl.) using the criterion of parsimony. The topologies were tabulated from the tree files using the program TreeCounter, written in C by me. Phylogenetic accuracy was scored with three measures: (1) the proportion of trees for which the relationship among an original set of four taxa was reconstructed correctly, (2) the proportion of trees that were completely correct, and (3) the proportion of correctly reconstructed branches among all trees.

The starting point for these analyses is a four-taxon tree known to have an inconsistent internal branch (Fig. 1), based on

previous analytical and simulation studies (Felsenstein, 1978; Huelsenbeck and Hillis, 1993). This tree has two long branches (length 0.5) and three short ones (length 0.05), where branch length is defined as the proportion of characters that are expected to change from one end of the branch to the other. Taxa were added to this tree according to the following rules: the longest branch(es) in the tree were identified, and a new taxon was joined at the midpoint of that longest branch. The length of the new branch was set such that the total length from the internal node to the tip was the same as for the original long branch (see Fig. 1). All distinct trees with between 4 and 15 taxa were used to simulate data. Although one might think that by adding taxa in this manner the number of possible distinct trees would steadily increase, instead it shows a wave-like increase and decrease as a function of number of taxa. This is because for particular numbers of taxa there is only one longest branch left in the tree, and thus there is only one possible tree that is one taxon larger. In contrast, in this single one-taxon-larger tree there are multiple equally longest branches, and thus there are several possible trees with yet one more taxon. In order to get an idea of what happens for large trees without dramatically increasing computation time, two relatively large trees were chosen for simulations: the single 22-taxon and 30-taxon trees. Note that these rules result in the creation of just a subset of all possible trees in the examined size range.

Data matrices of five sizes—10,000, 20,000, 40,000, 60,000, and 80,000 characters—were created by simulation across all trees. For one group of the trees, matrices of total size 1,000 characters were also created. For each tree, the total number of characters was kept constant as the number of taxa was increased, with the characters distributed equally among the taxa (for example, a total of 10,000 characters means that each of 4 taxa have 2,500 characters, each of 10 taxa have 1,000 characters, etc.). The proportions of variable and informative characters were determined by

the rate variation parameter, the length of the branches, and the number of taxa. Both proportions increased with the number of taxa. For example, for 4 taxa approximately 40–44% of the characters were variable and about 3–5% were informative, for 12 taxa approximately 54–64% of the characters were variable and 41–49% were informative, and for 30 taxa approximately 69–75% of the characters were variable and 59–65% were informative.

Trees were reconstructed according to the criterion of parsimony using equally weighted characters and heuristic searches with TBR branch swapping. For a limited group of data matrices, trees were also reconstructed using maximum likelihood. The model of evolution used for the maximum likelihood analyses matched perfectly the model under which the data were simulated: gamma shape parameter of 0.5, base frequencies equal, kappa of 2.

## RESULTS

The general result from all analyses was that, for a given total data matrix size, phylogenetic accuracy improved as the number of taxa increased. This relationship contradicts the notion that increasing the number of taxa should worsen rather than improve accuracy, and seems especially surprising given that as the number of taxa is increasing, the number of characters per taxon is decreasing. Nevertheless, there is a limit to this generalization—accuracy did worsen when the number of characters per taxon became quite low. In this study a strong decline in accuracy with increasing taxa was seen only in the smallest data matrices (above ~8 taxa for total matrix size of 1,000 characters; i.e., 125 characters per taxon; Fig. 2).

The specific results based on parsimony are described in more detail next. A final section compares the parsimony results with some maximum likelihood analyses.

### *Increasing the Number of Taxa and/or Characters*

For all data matrix sizes examined, when the total number of characters is held constant, accuracy improves with the addition

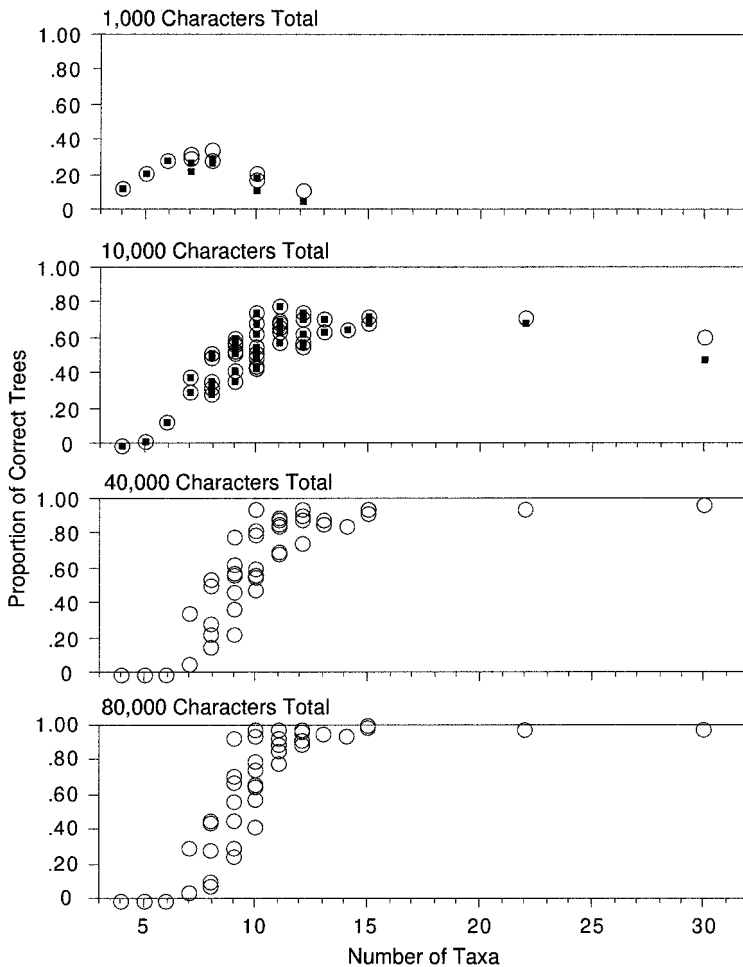


FIGURE 2. Two measures of phylogenetic accuracy: (1) the proportion of replicates resulting in trees that accurately represent the relationship among the original four taxa (○) and (2) the proportion of replicates resulting in completely correct trees (■), plotted as a function of number of taxa. The number of characters for each graph represents the total number across all included taxa (e.g., for 10 taxa there are 100 characters per taxon); thus within each graph the number of characters per taxon decreases as the number of taxa increases. From top to bottom: 1,000 characters total, 10,000 characters total, 40,000 characters total, 80,000 characters total. For 40,000 and 80,000 characters total the two measures are exactly equivalent, and thus only one set of symbols is plotted.

of taxa over all or at least some portion of the parameter space (Figs. 2, 3). Improvement was seen according to all three measures of accuracy: (1) the proportion of trees in which the relationship among the original four taxa is correct (Fig. 2), (2) the proportion of trees that are completely correct (Fig. 2), and (3) the proportion of correct branches among all trees (Fig. 3). The strongest decline in accuracy is seen using the second measure (proportion of com-

pletely correct trees), which declines with more than ~10 taxa for the smallest data matrix (1,000 total characters) and with more than ~20 taxa in the second smallest (10,000 total characters). There is also a slight decline in accuracy according to the first measure, proportion of trees with the correct four-taxon relationship, for the smaller data matrices. The third measure, proportion of correct branches among all trees, remains high because nearly all of

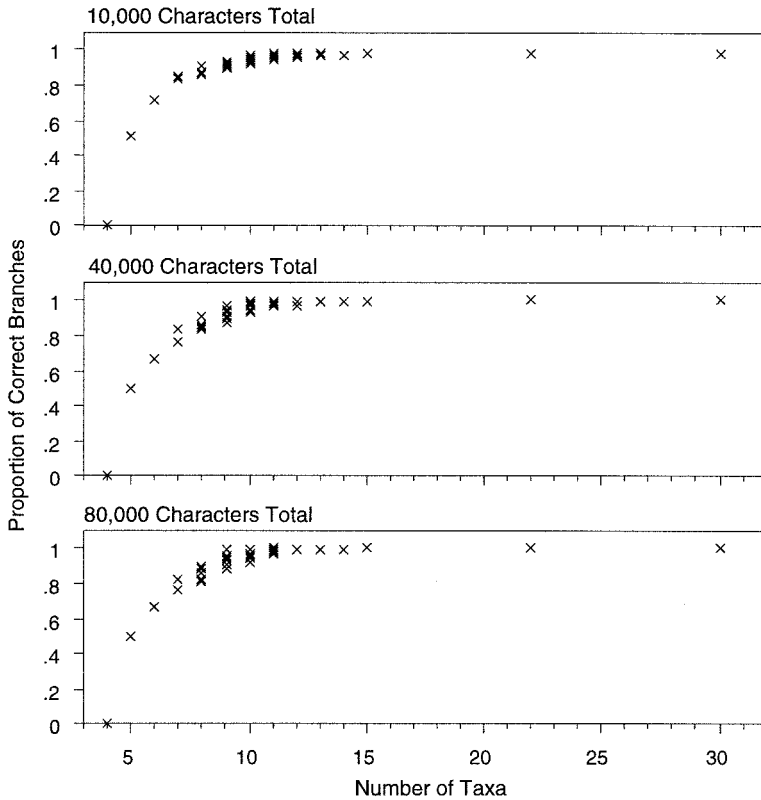


FIGURE 3. The proportion of correct branches reconstructed for three sizes of data matrices (10,000, 40,000, 80,000 characters total across all taxa) as a function of number of taxa. The number of characters per taxon decreases as the number of taxa increases.

the incorrect trees contain only one or two incorrect branches. Of course with a sufficiently low number of characters per taxon all measures of accuracy would be expected to decline.

These results suggest that it is always preferable to add taxa rather than characters. However, although it is true that accuracy improves more dramatically with addition of taxa, it also improves with an increase in the number of characters per taxon (Fig. 4), as long as there is no inconsistent branch in the tree. Inconsistent branches cause accuracy to decline with an increase in number of characters.

#### *Where Is It Most Helpful to Add New Taxa?*

Because of the rules followed for adding taxa to the original four-taxon tree, trees of a given number of taxa differ in their rel-

ative branch lengths. There was a strikingly wide range in the accuracy of phylogenetic reconstruction observed for these trees. The general pattern was that the trees reconstructed least accurately were those in which taxa were added closest to the tips of the long branches, and those reconstructed most accurately were those in which taxa were added closest to the base of those branches (Fig. 5). This result is consistent with the analytical result of Kim (1996), who found that an inconsistent internal branch could be made consistent if one taxon was added to each of the two long branches in approximately the basal third of those branches (the exact position depends on the relative branch lengths).

#### *Inconsistency*

By comparing the results for data matrices of different sizes, it is possible to get

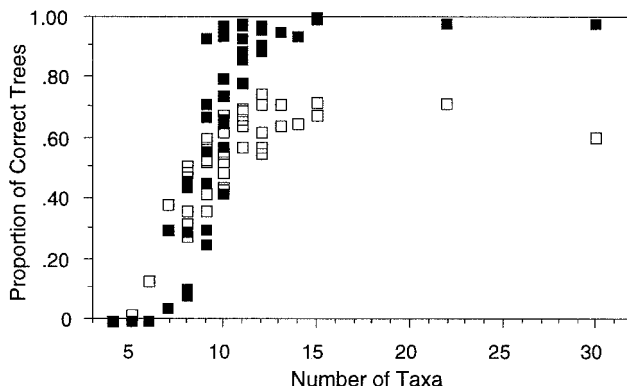


FIGURE 4. The proportion of replicates resulting in trees that accurately represent the relationship among the original four taxa for data matrices of total size 10,000 characters ( $\square$ ) and 80,000 characters ( $\blacksquare$ ) as a function of number of taxa, where the number of characters per taxon decreases as the number of taxa increases. These two data matrix sizes represent the complete extremes evaluated in this study; results from matrices of intermediate sizes fall between the values plotted here.

some insight into which trees have inconsistent internal branches (Fig. 4). It is clear that the trees of four, five, and six taxa have an inconsistent internal branch, because the larger data matrices all fail to reconstruct the correct four-taxon relationship 100% of the time. Certain of the trees of between 7 and 10 taxa seem to have an inconsistent internal branch, because the accuracy is worse with more data than with less. For all of the trees with more than 10 taxa inconsistency no longer appears to be a problem. However, because inconsistency is a condition based on infinite data, it is not possible to make definitive statements about this situation with the relatively small data matrices examined here.

#### *Maximum Likelihood*

Limited analyses using maximum likelihood show a different pattern than parsimony for the trees examined here. The major difference is that this method as implemented here does not suffer from problems with inconsistent branches, and thus it reconstructs the smaller trees in this study correctly (Fig. 6; also Hillis et al., 1994). Maximum likelihood also reconstructs the larger trees with higher accuracy than parsimony (Fig. 6), although it is not reasonable to compare these two meth-

ods in this case because the model of maximum likelihood evolution used for phylogeny reconstruction matched the model of evolution used to simulate the data much more closely than did the parsimony reconstruction model. Future work might compare various phylogenetic reconstruction methods more fairly, and determine if certain methods are more or less susceptible to taxon and character sampling.

#### DISCUSSION

Can we conclude that we always should add data in the form of taxa rather than characters? Under the conditions of this study, addition of both kinds of data improves phylogenetic accuracy, but when the total number of characters is held constant, accuracy is much higher if the characters are distributed across a larger number of taxa. Although the relationship between adding taxa versus adding characters was not examined directly by Lecointre et al. (1993, 1994), the general conclusion here is compatible with their result that the impact of species sampling was higher than expected, and it is also consistent with paleontological studies that found that taxa that break up long branches improve accuracy (Gauthier et al., 1988; Donoghue et al., 1989; Huelsenbeck, 1991).

The results of these simulations suggest that there are only a few reasons that one



FIGURE 5. The proportion of replicates resulting in trees in which the relationship among the original four taxa is correct, plotted as a function of number of taxa for two data matrix sizes (10,000 and 80,000 characters total, where the number of characters per taxon decreases as the number of taxa increases). The most accurate trees (▼) are those where new taxa had been added at the base of the long branches, and the least accurate trees (△) are those where new taxa were added toward the tips.

would not want to increase the number of taxa in a phylogenetic study. The first, and most obvious, is that no such taxa exist to sample. This may be because there have not been sufficient splitting events among the taxa of interest to create appropriate taxonomic units, or because such taxa have been lost through extinction, or even be-

cause splitting events occurred so rapidly in a narrow window of time that no taxa with sufficiently short branch lengths exist. The second is that strong support for the phylogenetic relationships in question exists and there is no interest or need to spend time and money obtaining data from other relatives. Of course an impor-

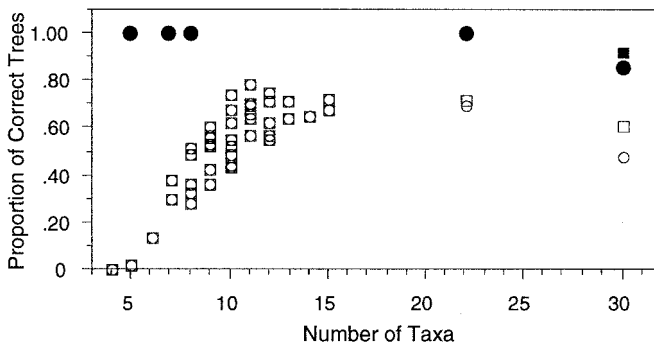


FIGURE 6. The proportion of replicates resulting in trees that accurately represent the relationship among the original four taxa (○, ●) and the proportion of replicates resulting in completely correct trees (□, ■), plotted as a function of number of taxa. Trees were reconstructed from data matrices of size 10,000 characters, and the number of characters per taxon decreases as the number of taxa increases. Open symbols are results using parsimony and closed symbols are results using maximum likelihood.

tant caveat in this case may be that the strong support is for *incorrect* relationships, in which case adding taxa might be critically important to improve accuracy. It therefore is important to explore the nature of support for particular relationships and to examine whether particular misleading phenomena might be affecting the result. For example, workers have determined that long-branch attraction can mislead phylogenetic reconstruction methods, as can base composition bias or other forms of nonrandom convergence in the data (Felsenstein, 1978; Huelsenbeck and Hillis, 1993; Lockhart et al., 1994; Swofford et al., 1996). It is possible to explore the possible impact of such phenomena using methods such as the parametric bootstrap, as outlined by Huelsenbeck et al. (1996).

An interesting third possibility is that the added taxa might make what was a consistent tree into an inconsistent tree. One could imagine this happening, for example, by the addition of successive outgroup taxa with a short internal branch between them. Consideration of this possibility serves to highlight the very particular nature of the conditions for adding taxa in this study: Taxa were added specifically to break up long branches. It would be entirely misleading to claim that this study supports a general conclusion that more taxa always improve phylogenetic accuracy.

Conversely, there seem to be very few reasons that it would be necessary to increase the number of characters applied to a particular phylogenetic question beyond some reasonable level (although that level may be quite a bit higher than that seen in many studies today). Obviously there does exist some threshold below which the number of characters is insufficient. According to the conditions of this study that level is quite low, but it is likely to be higher with real data where in general overall rates of evolution are slower and the proportion of variable characters is lower. A second reason might be that the available data are effectively useless because they have not evolved at a rate appropriate for the question of interest (e.g., the DNA sequences are saturated). This determination,

however, may largely be a question of context, because with sufficient taxa in the right parts of the tree apparent homoplasy would disappear. Nonetheless, for certain questions there is undoubtedly some kind of balance between getting "bad" data from more taxa in the hopes that these taxa will solve the problems with the data, and looking for different data. More work in this area is needed. In some situations it can be very difficult to obtain data from new sources (e.g., different genes), and it could make sense to work first on including more taxa, and only then to move to new sources of characters.

An encouraging conclusion from this study is that the accurate reconstruction of large trees, such as the large-scale studies of angiosperm relationships (Chase et al., 1993), may be easier than previously thought, because such trees are less likely to have very long branches. In fact, big trees may be far easier to reconstruct accurately than small ones, as demonstrated dramatically in recent simulations (Hillis, 1996; Purvis and Quicke, 1997). Although this result contradicts the message of Kim's (1996) paper, it is not inconsistent with his results. Several caveats regarding this conclusion are warranted, most important of which is the recognition of the very particular conditions of this study where taxa were added specifically to break up long branches. If taxa were instead added randomly with respect to branch length, as might be more realistic, the expectation is that phylogenetic accuracy would also improve but more slowly. Nonetheless, we are generally not completely in the dark about the identity of potentially long branches, and it is certainly conceivable that we can add taxa selectively to purposely break them up.

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