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Points of View

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Combining Data Sets with Different Numbers of Taxa for Phylogenetic Analysis

JOHN J. WIENS[1] AND TOD W. REEDER[2]

Department of Zoology, University of Texas, Austin, Texas 78712-1064, USA

Paralleling the spread of molecular systematics in recent years has been growing concern over how to integrate morphological and molecular data in phylogenetic analysis (e.g., Miyamoto, 1985; Hillis, 1987; Kluge, 1989; Barrett et al., 1991; Shaffer et al., 1991; Swoffford, 1991; Donoghue and Sanderson, 1992; Bull et al., 1993b; de Queiroz, 1993; Eernisee and Kluge, 1993; Kluge and Wolf, 1993; Chippindale and Wiens, 1994; Huelsenbeck et al., 1994; Wiens and Chippindale, 1994). A powerful approach for dealing with diverse data sets involves pooling all the available data and finding a globally parsimonious solution. This has been termed the combined (de Queiroz, 1993), total evidence, or character congruence approach (Kluge, 1989). A potential problem when combining diverse characters into a single matrix is that the taxonomic coverage of the separate data sets may not overlap completely. Thus, some taxa may lack data of one type or another in a nonrandom fashion. Should these "incomplete" taxa be included in a combined analysis?

There have been relatively few phylogenetic analyses in which diverse data sets (such as molecular and morphological data) have been combined (see Chippindale and Wiens, 1994, for a recent review). In most analyses in which the separate matrices did not include exactly the same taxa (e.g., de Sá and Hillis, 1990; DeSalle et al., 1992; Vane-Wright et al., 1992; Hillis et al., 1993; Olmland, 1994; Weller et al., 1994; Yoder, 1994), the authors excluded the taxa for which one of the data sets was unavailable (in the studies listed above, those taxa lacking molecular data). The only explanation given for this omission (Vane-Wright et al., 1992) was the desire to avoid a preponderance of missing data in the combined matrix. Although this concern is legitimate (e.g., Platnick et al., 1991), there is growing support for the idea that incomplete taxa can be informative in phylogenetic analysis (e.g., Doyle and Donoghue, 1987; Gauthier et al., 1988; Donoghue et al., 1989; Novacek, 1992). In three recent papers, authors have included taxa scored only for morphological data in combined analyses with molecular data (Eernisse and Kluge, 1993; Wheeler et al., 1993; Vrana et al., 1994).

There are reasonable justifications both for including and excluding incomplete taxa. There are two ways in which the inclusion of incomplete taxa might confound an analysis: they may increase the number of equally parsimonious trees obtained, or they may cause an incorrect tree to be chosen as the most-parsimonious tree. Pale-

[1] Present address: Section of Amphibians and Reptiles, Carnegie Museum of Natural History, Pittsburgh, Pennsylvania 15213, USA. E-mail: wiensj@clpgh.org.

[2] Present address: Division of Amphibians and Reptiles, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA.

ontological studies (e.g., Rowe, 1988; Novacek, 1992) and computer simulations (Huelsenbeck, 1991) have documented that adding highly incomplete taxa can increase the number of equally parsimonious trees. A large number of shortest trees can obscure relationships among both the complete and incomplete taxa.

A more serious concern is that adding incomplete taxa might also lead to an incorrect tree being chosen as the most-parsimonious tree. Computer simulations (Huelsenbeck, 1991) have shown that adding incomplete taxa decreases the probability of finding the correct tree, relative to adding complete taxa (when the taxa are of equivalent age). However, these simulations did not address whether or not accuracy (the probability of estimating the true phylogeny) would be improved or worsened by adding incomplete taxa versus excluding them.

There are three main reasons for including incomplete taxa. First, including incomplete taxa permits a hypothesis of relationships for all the members of a group, not just the ones for which complete data are available. A phylogenetic hypothesis for all the taxa within a group is desirable for comprehensive taxonomic revisions and for rigorous analyses of character evolution, evolutionary rates, coevolution, and biogeography.

Second, the inclusion of additional taxa may improve the chances of estimating the right tree. Hendy and Penny (1989) and Swofford and Olsen (1990) recommended including additional taxa as a way to subdivide the long, unbranched lineages of a phylogenetic tree. Long branches tend to be linked by parsimony analysis, regardless of the actual relationships of the lineages (e.g., Huelsenbeck and Hillis, 1993), and addition of more characters may only further support the incorrect grouping (Felsenstein, 1978). Computer simulations by Wheeler (1992) showed that inclusion of all the relevant taxa is the single most important factor in obtaining a tree consistent with the correct phylogeny, whereas the amount of missing data (10%, 15%, or 25% missing) has no significant effect on accuracy. In Wheeler's (1992) study, however, the missing data were randomly distributed across cells in the matrix, and no taxa were particularly incomplete relative to others. This situation clearly is not comparable to the problem presented by incomplete taxa.

A third justification for including incomplete taxa is the principle of total evidence. According to this general philosophical principle (e.g., Carnap, 1950; Hempel, 1965), the best hypotheses are those that explain all the relevant data simultaneously (Kluge, 1989). In the context of systematics, this approach requires including all relevant taxa and characters (Gauthier et al., 1988; Kluge, 1989). However, the hypothesis that most parsimoniously explains all the data may not be the one that best reflects the true phylogeny.

In this study, we address the problem of combining data sets with different numbers of taxa for phylogenetic analysis; specifically, whether it is better to include or exclude those taxa that are missing data from one or more sets of characters. The most important criterion for evaluating the consequences of including these taxa is whether their inclusion causes the resulting phylogenetic estimates to be more or less similar to the true phylogeny (i.e., more or less accurate). However, accuracy can be addressed in only a few cases, using computer simulations and laboratory-produced phylogenies (Hillis et al., 1992). A useful criterion that can be applied to a variety of real data sets is whether the inclusion of the incomplete taxa leads to trees that are more or less similar to the tree based on the complete data (if it could somehow be obtained). If the trees including the incomplete taxa differ greatly from the complete tree, then their inclusion may be a source of error in phylogeny reconstruction (regardless of whether the complete tree is right or wrong). However, if there is little effect from including complete versus incomplete taxa, the inclusion of incomplete taxa may be relatively harmless.

We addressed both of these questions through a series of subsampling experi-

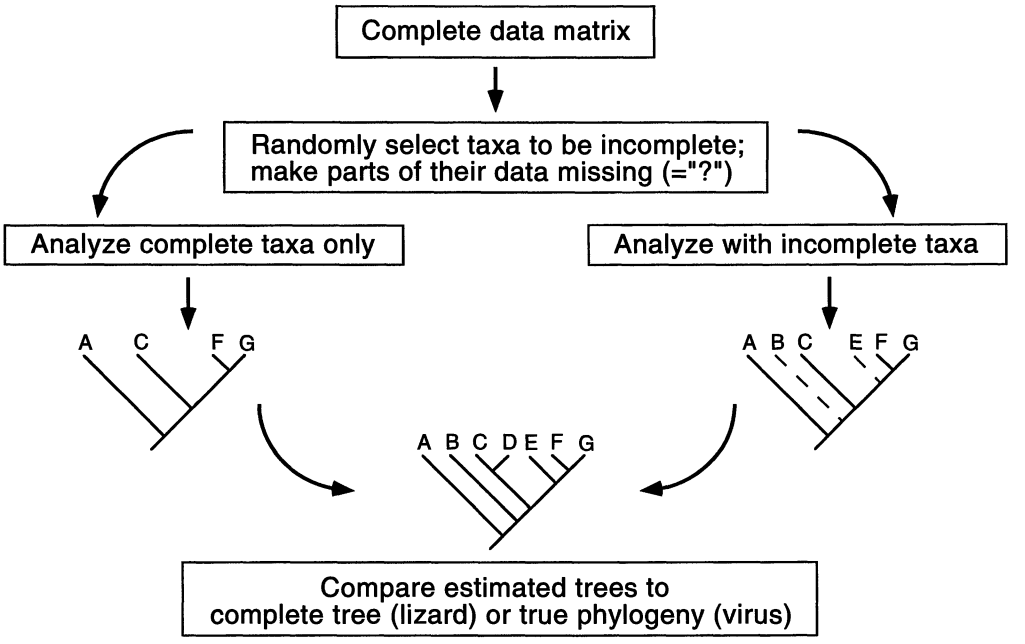

FIGURE 1. Generalized methodology used in this study for examining the effects of including incomplete taxa in phylogenetic analysis.

ments using two empirical systems: (1) phrynosomatid lizards, for which we have both molecular and morphological data for a large number of species (40; Reeder and Wiens, 1996), and (2) the bacteriophage virus T7, using a known phylogeny of nine strains generated in the laboratory for which there is both DNA sequence and restriction-site data (Hillis et al., 1992; Bull et al., 1993a). The general protocol for these experiments (Fig. 1) involved (1) randomly selecting certain taxa to be complete and others to be incomplete, (2) making taxa incomplete by replacing one of their sets of characters with missing data, (3) analyzing the complete taxa alone and with the addition of incomplete taxa, and (4) comparing the similarity of the trees with and without incomplete taxa to the complete or correct phylogeny.

EXPERIMENTS WITH LIZARDS AND VIRUSES

Lizard Data and Methods

The raw data for the experiments with phrynosomatid lizards consisted of 134 phylogenetically informative morphological characters (squamation, osteology, coloration, karyology, life history) and 111 informative molecular characters (109 DNA nucleotide substitution characters from the mitochondrial 12S and 16S ribosomal genes and 2 allozyme characters) for 40 species of phrynosomatid lizards, representing all 10 genera in the family. (Details of characters, taxa, specimens, and methods used will be published elsewhere [Reeder and Wiens, 1996]. The annotated data matrix is available on disk from J.J.W.) Data matrices were subjected to parsimony analysis using PAUP 3.0s (Swofford, 1990), with all characters weighted equally.

Sets of species were selected from the complete set of 40 taxa (using a random number table) to be complete taxa. The remaining species in each matrix were then rendered incomplete by coding their molecular data as missing (i.e., "?"). The complete taxa were analyzed alone and with the inclusion of randomly selected sets of incomplete taxa. To control for the overall number of taxa in the analysis, incomplete taxa were added to different numbers of

complete taxa: 5 and 15 incomplete taxa were added to 5 complete taxa; 10, 20, and 30 incomplete taxa were added to 10 complete taxa; 10 and 20 incomplete taxa were added to 20 complete taxa; and 10 incomplete taxa were added to 30 complete taxa. Ten replicate matrices were created for each level (5, 10, 20, 30) of complete taxa. For comparison, 10 trials were performed in which 10 complete taxa were randomly chosen, 10 and 20 complete taxa were added to them, and the resulting trees were compared with the tree based on 40 complete taxa.

The trees derived from these analyses were then compared with the tree of 40 complete taxa (with taxa pruned so as to be comparable). Similarity between trees was assessed using the consensus fork index (Colless, 1980), which is the number of clades in common between the two trees divided by the total number of nontrivial clades possible (the number of taxa minus 2). When multiple equally parsimonious trees were generated from a search, each of the shortest trees was compared with the complete tree and the average similarity was used.

Only the molecular data alone were chosen to be deleted because in real situations where molecular and morphological data are combined the molecular characters are consistently the ones that are entirely missing for a given taxon (there are few taxa known from molecular data but not morphological data). Searches were conducted using the branch-and-bound option for 5 and 10 taxa and using the heuristic search option (random addition sequence, 20 replicated searches) for larger numbers of taxa. Statistical analysis of the results (multiple regression) was performed using the Statview™ software package.

Virus Data and Methods

The raw data for the virus analyses consisted of 87 phylogenetically informative restriction-site characters (from Hillis et al., 1992) and 30 informative DNA nucleotide substitution characters (from Bull et al., 1993a) scored for nine viral strains. These raw data sets were enlarged or reduced by random subsampling or resampling of characters to make three new data matrices in which the numbers of characters of each class were equal but the total number of characters differed: one with 10 characters of each type, another with 30 of each type, and a third with 87 of each type (data matrices are available from J.J.W. in annotated electronic format).

For each data matrix, viral strain R was used as an outgroup (following Hillis et al., 1992), and three other viral strains were chosen randomly and designated as complete. The remaining five taxa were made incomplete by replacing their restriction-site or DNA sequence data with missing data. The complete taxa were analyzed alone and then with the sequential, random addition of the five incomplete taxa. All of the resulting trees were compared with the correct phylogeny for these taxa. Accuracy was measured as the proportion of resolved nodes in common between the estimated trees and the correct phylogeny, using the average consensus fork index (Colless, 1980). Twenty random selections of taxa were performed for each data matrix, 10 in which the DNA sequence data were missing in the incomplete taxa and 10 in which the restriction-site data were missing. Phylogenetic analyses were performed using PAUP 3.1+6 (Swofford, 1993), with each restriction-site and DNA sequence character receiving equal weight. Following Hillis et al. (1992), restriction-site gains and losses were weighted equally.

In the preceding virus analyses and in the lizard analyses, all of the incomplete taxa had approximately 50% of their characters missing. To address the effects of different levels of completeness on accuracy, a series of subsampling experiments were performed on the virus restriction-site and DNA sequence data sets separately, replacing various numbers of characters in each data set with missing data. For the restriction-site analyses, 7 randomly selected characters were deleted from the set of 87 informative characters to make the overall number of characters more easily divisible. As in the previous virus analy-

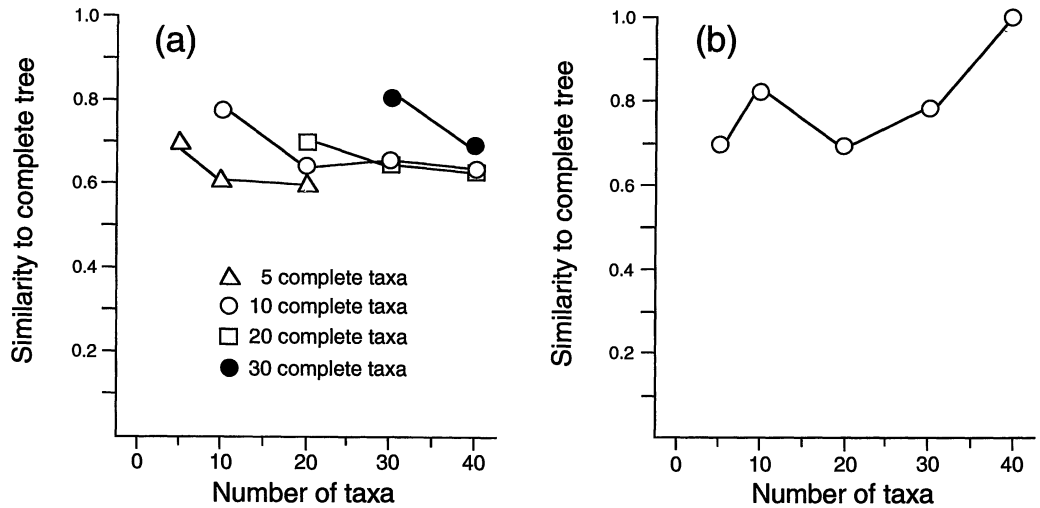

FIGURE 2. Effects of including and excluding incomplete taxa (missing molecular data) and complete taxa on the similarity of estimated trees to the trees based on the complete molecular and morphological data for phrynosomatid lizards. (a) Effects of including incomplete taxa. Symbols represent the average similarity between the tree based on 40 complete taxa and the tree(s) from sets of complete taxa with different numbers of incomplete taxa included. For example, the filled circle on the left represents the mean similarity to the complete tree based on 30 complete taxa only, whereas the filled circle on the right represents the similarity with 30 complete taxa and 10 incomplete (morphology-only) taxa added. Each symbol represents the mean accuracy for 10 random selections of taxa. (b) Effects of including and excluding complete taxa. Open circles show the mean similarity for 10 replicates (random selections of taxa).

ses, the outgroup (strain R) and three randomly selected taxa were chosen to be complete. The remaining taxa had various proportions of the 80 restriction-site characters randomly selected and replaced by missing data. Ten random selections of taxa (with concomitant random selections of characters) were performed for each of four different levels of completeness; 25% complete (i.e., 60 characters missing data), 50% complete, 75% complete, and 100% complete (no characters missing data, complete taxa subtracted and added). The resulting trees were compared with the true phylogeny to assess the effects of taxon completeness on accuracy. A set of similar experiments were carried out on the DNA sequence data. Two randomly selected characters were deleted from the set of 30 informative characters to make the numbers of characters more easily divisible, and 10 random selections of taxa were performed for each level of completeness (25%, 50%, 75%, 100%).

Lizard Results

The major results of the subsampling experiments are shown in Figure 2. When all the taxa were compared (complete and incomplete taxa), adding incomplete taxa (on average) decreased the similarity of the resulting trees to the tree based on all the data (Fig. 2a). The results in Figure 2a were subjected to multiple regression analysis (with $n = 120$ random selections of taxa), with similarity to the complete tree as the independent variable and completeness and total number of taxa as dependent variables. This analysis revealed a significant correlation ($P = 0.0001$) between similarity to the complete tree and the proportion of included taxa that were complete but not between similarity and the total number of taxa ($P = 0.276$).

The results of including and excluding only complete taxa are surprising (Fig. 2b). Although one might expect the similarity of these trees to the complete (40 taxon) tree to increase with increasing numbers of

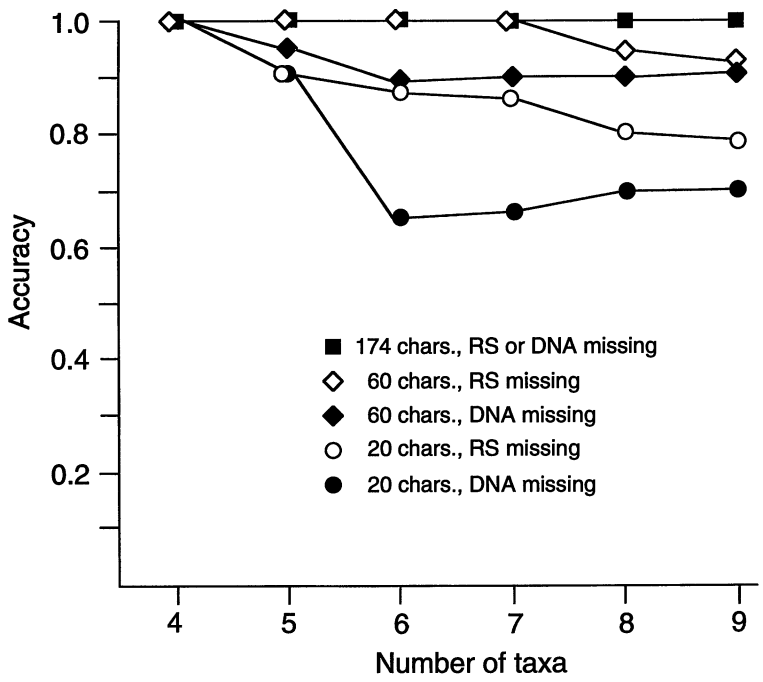

FIGURE 3. Effects of including taxa scored for only one data set on the accuracy of phylogenetic analysis using combined data sets, based on analyses of published DNA and restriction-site (RS) data for a known phylogeny of nine viral strains (Hillis et al., 1992; Bull et al., 1993a). Each point represents the average accuracy from 10 random selections of taxa for each data matrix. Accuracy is the proportion of reconstructed nodes shared with the true phylogeny. Four of the nine taxa are complete (no data missing), whereas the other five have either all of their RS or DNA sequence data coded as missing.

complete taxa added, there was a sharp decrease in similarity between 10 and 20 taxa, and the similarity to the complete tree is less for 30 taxa than for 10. Thus, even adding complete taxa does not always increase the similarity to the tree based on all the data. Presumably, as the number of taxa increases the number of possible trees increases, and it becomes harder to infer all details of the phylogeny "correctly" (Swofford and Olsen, 1990). Thus, when more taxa are included, the more chances there are to be wrong somewhere in the tree. The unusual pattern of similarity rising and falling and rising again with the increasing number of taxa might be explained by the fact that additional taxa are most likely to improve estimation when the total number of taxa is smallest and branches are longest (and potentially misleading). As more taxa are added, there ceases to be a benefit to subdividing branches, and the addition of more taxa only decreases the similarity to the complete tree.

Virus Results

The results of the virus analyses are shown in Figures 3 and 4. As suggested by the lizard analyses, inclusion of the incomplete taxa leads to a small but consistent decrease in accuracy relative to exclusion of these taxa. The magnitude of this decrease is sensitive to three parameters that were not changed in the lizard study: (1) the type of data missing (restriction site or DNA sequence), (2) the total number of characters in the analysis, and (3) the proportion of characters missing data (0%, 25%, 50%, 75%). In general, the decrease in accuracy is greater when the sequence data rather than the restriction-site data are missing. This difference might be due to the greater homoplasy in the restriction-

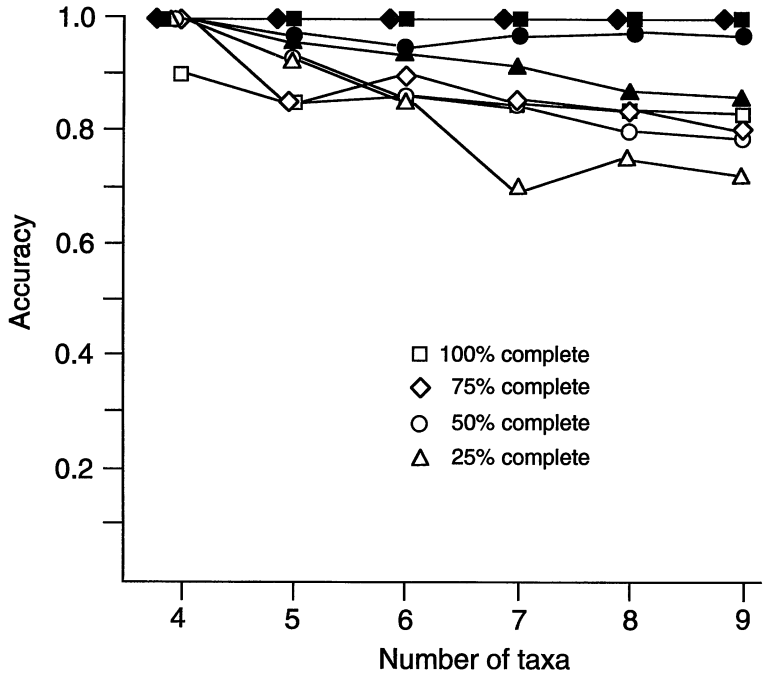

FIGURE 4. Effects of different levels of completeness (proportion of characters not missing data) on the accuracy of phylogeny reconstruction, based on separate analyses of published DNA and restriction-site data for a known phylogeny of nine viral strains (Hillis et al., 1992; Bull et al., 1993a). Each symbol represents the average accuracy from 10 replicated matrices. Open symbols represent results from analyses of 28 DNA sequence characters; filled symbols are results from analyses of 80 restriction-site characters. Accuracy is the proportion of resolved nodes shared with the true phylogeny. Four of the nine taxa are complete (no data missing), whereas the other five have different proportions of characters replaced by missing data.

site data than in the sequence data; the sequence data has a retention index (RI) of 0.947 (consistency index [CI] = 0.909; rescaled consistency index [RCI] = 0.861), whereas the restriction-site data has an RI of 0.810 (CI = 0.750; RCI = 0.608). These analyses suggest that the larger the number of characters in the analysis, the smaller the cost in accuracy associated with including incomplete taxa. For example, in the data matrices with 87 characters of each type, there is no decrease in accuracy when incomplete taxa are included. Although accuracy does appear to be sensitive to levels of completeness, the proportion of characters that lack data has surprisingly little effect on accuracy. For both the restriction-site data and DNA sequence data, accuracy is very similar when the added taxa are 50%, 75%, and 100% complete (Fig. 4). Although accuracy is markedly lower for taxa that are 25% complete, most nodes are still reconstructed correctly, even when three quarters of the characters are missing data.

DISCUSSION

To Include or Not to Include?

Our results from the lizard and virus analyses suggest that including taxa that are missing data from one or more data sets in a combined analysis decreases the similarity of the resulting trees to the phylogeny based on the complete data and to the true phylogeny. However, this decrease appears to be minor. Even when the number of characters was relatively small (nearly equal to the number of taxa) and the proportion of missing data was large (75%), most nodes were nevertheless reconstructed correctly using the T7 data.

Based on these results, we favor including these incomplete taxa in phylogenetic analyses of combined data sets. Although there is potentially a cost associated with including these incomplete taxa, there can be a similar cost to including complete taxa (see Figs. 2b, 4). We prefer to have a phylogenetic hypothesis for these incomplete taxa that is mostly right rather than having no hypothesis for them at all.

Some might disagree as to what constitutes an acceptable decrease in accuracy and whether a decrease is acceptable at all. This is a fundamental and unresolved question in evaluating different approaches to phylogenetic inference (e.g., combined vs. separate analyses; Chippindale and Wiens, 1994). Confidence in the accuracy of phylogeny reconstruction will be more important in some cases than in others (e.g., phylogenetic studies of viral transmission vs. taxonomic revisions) (Swofford, 1991). In all cases, the first step is to be aware of these ambiguities and to make the users of phylogenetic hypotheses (e.g., evolutionary biologists, medical researchers, other systematists) aware of them also.

Another consideration is that these results are based on only two data sets. However, the overall similarity of the results between the two empirical systems and the great differences between the systems (e.g., vertebrates vs. viruses, morphological vs. molecular data sets), despite changes in various parameters within the virus system (e.g., proportion of missing data, number of characters, types of characters, levels of homoplasy), seem to support the generality of our conclusions. More studies are needed to assess the impact of including incomplete taxa under a wider variety of conditions. The subsampling protocol we used for the phrynosomatid lizard data may be useful for addressing this problem in other organisms. Computer simulations will also provide useful insights.

Other Options

Besides simply including or excluding the incomplete taxa in the combined analysis, there are a number of other ways to deal with the problem of combining data sets with different numbers of taxa. For example, given a group in which there are morphological data for all the members but molecular data for a smaller number of taxa, one could combine and analyze the data for only the complete taxa and then infer the relationships of the incomplete taxa based on their relationships in the tree derived from morphology only (see Fig. 5a for a hypothetical example). This procedure requires a certain level of congruence between the results of the combined and the morphological analyses; otherwise, the placement of the incomplete taxa will be completely ambiguous (Fig. 5b). Furthermore, simply mapping a taxon onto a tree a posteriori does not require that its placement be the most-parsimonious one possible, because the relative cost of different positions (in terms of tree length) cannot be evaluated unless these taxa are included.

This mapping procedure was problematic in our analyses of phrynosomatid lizard phylogeny (Reeder and Wiens, 1996), in which the data consist of molecular characters scored for 40 species and morphological characters scored for the same 40 species plus 19 additional species. Comparison of the combined 59-taxon tree (including molecular and morphological characters and complete and incomplete taxa) with the tree based on morphological data alone revealed numerous differences in the placement of the incomplete (morphology only) taxa. These differences suggest that the molecular and morphological data can interact to change the hypothesized relationships of the morphology-only taxa. Apparently, the addition of the molecular data changes the relationships of the complete taxa, and these differences in the position of the complete taxa make alternative relationships more parsimonious for the morphology-only taxa. This situation is illustrated with a hypothetical example in Figure 6. Because novel interactions are likely between data sets when combined (Chippindale and Wiens, 1994), it seems unwise to try to map the position

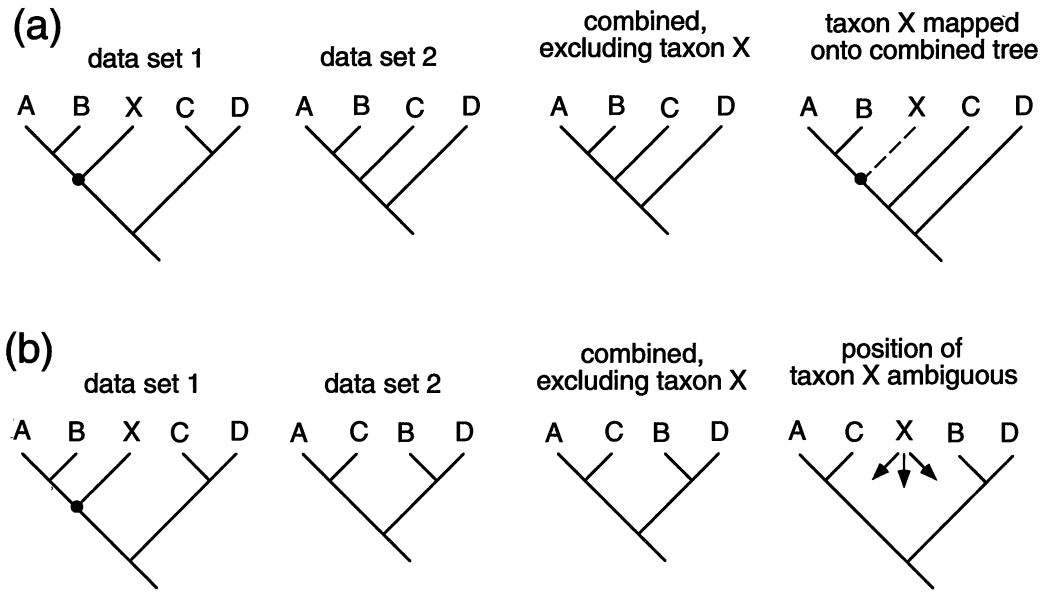

FIGURE 5. Trees for a hypothetical example that includes a taxon (X) scored for only one of two data sets. (a) The relationships of taxon X can be estimated without including that taxon in an analysis of the combined data if there is sufficient congruence between the data sets. (b) The position of taxon X cannot be estimated a posteriori because of incongruence between the data sets.

of the incomplete taxa onto a combined tree based on the relationships that have been determined using only one set of characters.

A similar approach involves combining data from several species sampled for different data sets into a single taxon, which can then be entered into the analysis as a complete "hybrid" taxon, corresponding to a higher group whose monophyly is supported by previous analyses (e.g., Miyamoto and Goodman, 1986). With this method, the monophyly of the higher taxon must be assumed, rather than allowing the analysis to test the monophyly of this taxon or to address the relationships of the species within it. However, in analyses of well-established higher level groups, this method seems useful for reducing the number of incomplete taxa without discarding data.

A seemingly conservative solution to the problem of including incomplete taxa might be to include them in the analysis but prune them out afterwards to obtain a phylogenetic estimate for the complete taxa only. This approach follows the suggestion of Swofford and Olsen (1990) that additional taxa be included (to subdivide long branches) but then removed after the analysis and seems to reap the benefits of including additional taxa without attempting to hypothesize relationships for taxa that are incomplete. Our results from the lizard and virus data suggest that this pruning approach does yield trees that are more similar to the complete or correct phylogeny than are the trees produced when all the taxa are included. The disadvantage of this approach is that it does not address the relationships of the incomplete taxa.

Another possible solution might be to exclude those data sets scored for only a limited number of taxa. This approach also reduces the amount of missing data in a matrix and seems to be widely used. Although inclusion of taxa alone is unlikely to be positively misleading (there are no bad taxa, only bad characters—incomplete taxa are only misplaced phylogenetically through a combination of homoplasy and

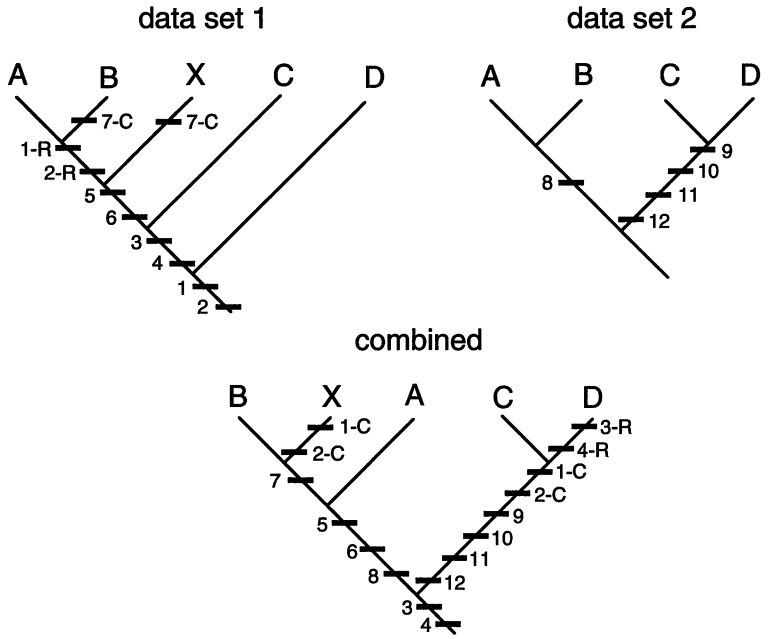

FIGURE 6. Hypothetical example showing how different data sets, when combined, interact to change the placement of a taxon (X) scored for only one of the data sets. When data sets 1 and 2 are combined, the characters in data set 2 constrain C and D as sister taxa. Because C and D are sister taxa, characters 1 and 2 (in data set 1) do not reverse to unite A and B to the exclusion of X. Thus, X is most parsimoniously placed as the sister taxon of B, even though data set 1 supports A and B as sister taxa and X is missing data for all the characters in data set 2. Bars = character-state transformations; C = convergent/parallel acquisition of a derived state; R = reversal to the primitive state.

ambiguity), addition of certain sets of characters certainly can be misleading because of homoplasy. However, we see no way in which the mere incompleteness of the characters can positively mislead. There may be a variety of reasons why one might want to exclude a set of characters from phylogenetic analyses (e.g., ambiguous sequence alignment, nonindependence), but excluding characters because of incompleteness alone may lead to unnecessarily discarding useful phylogenetic information.

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