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Weighting, Partitioning, and Combining Characters in Phylogenetic Analysis

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The number and diversity of characters available for phylogenetic analysis are increasing at a remarkable rate. Two general approaches have been advocated for integration of data from different sources (e.g., morphology and molecules, different genes or regions of a given gene, etc.). One of these approaches is taxonomic congruence (Mickevich, 1978), which involves three steps (Jones et al., 1993): (1) partitioning of the data into different "types," (2) separate phylogenetic analyses of the data in each of the partitions, and (3) construction of a consensus tree that summarizes the topological features shared among the trees that result from the separate analyses. The other approach is that of character congruence (Kluge, 1989; also known as the combined or total evidence approach), which consists of simultaneous analysis of all the available character data (Miyamoto, 1985; Kluge, 1989).

Bull et al. (1993; hereafter referred to as Bull et al.) and de Queiroz (1993; hereafter referred to as de Queiroz) recently advocated a third approach, which incorporates features of both taxonomic and character congruence. This approach is based on the premise that it is inappropriate to combine data sets in a single analysis if the trees that result from separate analyses of these data sets (partitions) are significantly different from one another ("heterogeneous" sensu Bull et al.) or are strongly supported and in conflict (de Queiroz). We refer to the approach advocated by Bull et al. and de Queiroz as the prior agreement approach.

In this paper, we argue that the objections that Bull et al. and de Queiroz raised against combined analyses, and the examples that they gave, either can be accommodated by differential character weighting or involve conditions that also will mislead the prior agreement approach. Bull et al. acknowledged weighting as a possible way to accommodate different evolutionary processes (under some circumstances) but did not address this approach in their arguments against data combination. We also discuss several potential problems of the prior agreement approach.

WHAT IS WRONG WITH COMBINING DATA?

Bull et al. argued that combination of diverse data may be inappropriate because different subsets of the characters may have evolved under different rules; thus, the results of a combined analysis could be misleading. We argue that differences in the "rules" of character evolution can be accommodated by differential character weighting in the context of a combined analysis of all the data. Differential weighting of characters certainly is not a new idea (e.g., Felsenstein, 1981), and its use in the context of combination of diverse data sets was suggested by Hillis (1987) and Barrett et al. (1991). This approach has the advantage that it simultaneously uses all the available characters and incorporates the relevant information on the processes of

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character evolution. The only situation in which appropriate character weighting could not lead to the correct tree is the case in which all data sets are positively misleading, but such circumstances would mislead the prior agreement approach as well.

Bull et al. stated that differential weighting may be appropriate only if significantly different trees have been obtained because of different "rates of change or transformational probability" in the different partitions of the total data (p. 394). But, these two causes would account for most cases of heterogeneity, including those in the computer simulations and analytical studies presented by Bull et al.

All of Bull et al.'s analyses involved different rates of evolution in different subsets of the data, and in each, all characters were weighted equally when the characters were combined. But use of appropriate weighting (e.g., giving less weight to characters evolving at fast rates or at rates that vary greatly among lineages) should lead to recovery of the correct phylogeny about as often as when the "best" (in Bull et al.'s examples, the most slowly evolving) characters are used alone. The estimate can even be improved by using appropriate weighting, because phylogenetic information from the rapidly evolving data set is added. For example, when the simulation shown in Bull et al.'s figure 3a (equal numbers of rapidly and slowly evolving characters) was performed with the rapidly evolving characters weighted by 0.2, the combined data recovered the correct phylogeny more often than when the slowly evolving characters were used alone (Fig. 1). From their analyses, Bull et al. concluded that "combining data may greatly worsen the phylogeny estimate" (p. 394) because "addition of a data set of rapidly evolving characters can change a correct estimate of the tree to an erroneous one" (p. 391). However, one could just as easily conclude that adding slowly evolving characters to a set of rapidly evolving characters improves the estimate.

De Queiroz's (1993) sole objection to combined analyses applied to cases in which there is nonindependence of characters within data sets (see also Shaffer et al., 1991; Swofford, 1991). Yet, nonindependence of characters is simply a problem of character weighting (Donoghue and Sanderson, 1992)—a character is given more weight than appropriate (relative to completely independent characters) because its probability of transformation to a particular state is linked to that of other characters. When nonindependence is hypothesized, the characters under suspicion can be weighted to reflect their lesser value as independent phylogenetic evidence. For example, weighting sets of characters to reflect their presumed nonindependence recently has been advocated by Wheeler and Honeycutt (1988) and Dixon and Hillis (1993) for ribosomal DNA sequence data. For cases of lateral gene transfer, Doyle (1992) recommended an extreme weighting scheme, in which the phylogeny implied by the sequences from a given gene is coded as a single character and included in a combined analysis.

Most of the arguments that have been made against data combination involve violations of basic assumptions of the inference method. However, separate analyses use the same inference method as do combined analyses and therefore are sensitive to the same assumptions. For example, parsimony analysis makes at least the following assumptions: (1) independence of characters, (2) independence of lineages (e.g., no hybridization, introgression, or lateral transfer of genes), and (3) similar rates of change along branches of the tree (Felsenstein, 1978; see also Hendy and Penny, 1989; Zharkikh and Li, 1993). Bull et al. and de Queiroz presented the same case of lateral gene transfer (Dykhuizen and Green, 1991), a situation of nonindependence of both lineages and characters, as an argument for not combining data. Bull et al. stated that "a combined analysis can yield an erroneous estimate of phylogeny with increasing certainty as data set size increases" (p. 385) (i.e., the data are inconsistent), and one set of their computer simulations (the results of which are shown in their fig. 4) involved combination of sets

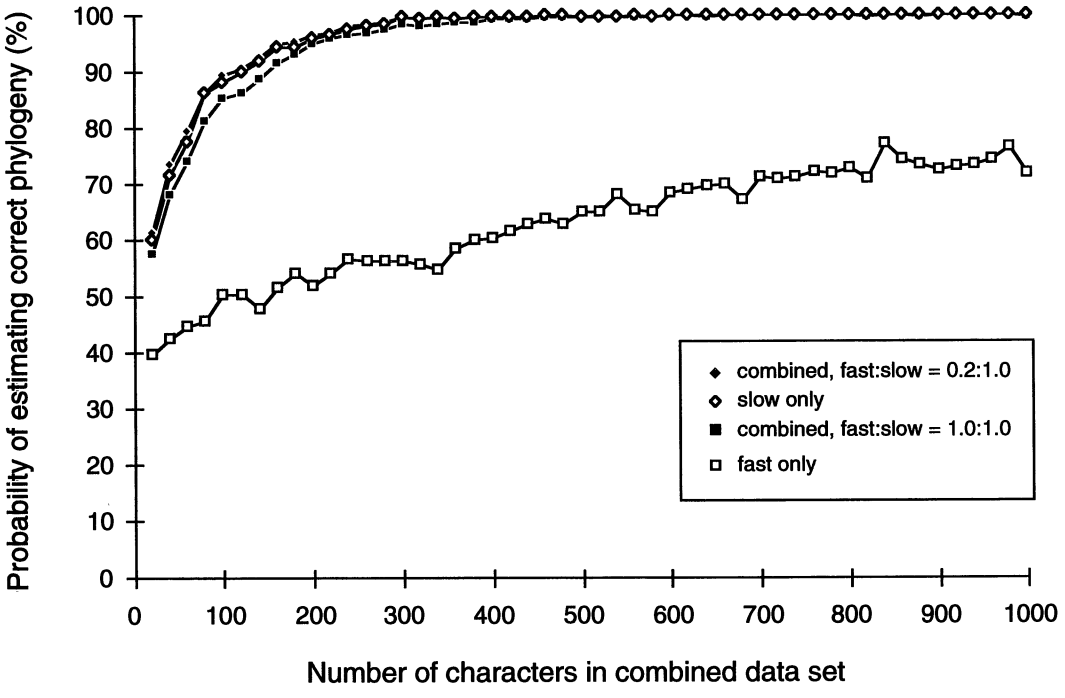

FIGURE 1. Phylogenetic estimation using appropriate weighting of combined data sets can be better than separate analyses of the data sets. The simulations shown in Bull et al.'s (1993) figure 3a were repeated, using several different combinations of weights. The rapidly and slowly evolving data sets had equal numbers of characters, and characters in each data set were given the following relative weights (slow : fast and fast : slow): 0:1.0, 0.2:1.0, 0.4:1.0, 0.6:1.0, 0.8:1.0, and 1.0:1.0. (Cases in which one of the data sets was weighted by 0 were equivalent to using only one of the data sets.) Giving more weight to the rapidly evolving characters than to the slowly evolving characters worsened estimation relative to equal weighting of characters, whereas weighting rapidly evolving characters less than the slowly evolving characters improved estimation. The weight ratio (fast : slow) of 0.8:1.0 usually worsened estimation relative to use of slowly evolving characters alone. The weight ratio 0.6:1.0 gave results similar to those from the slowly evolving characters alone, whereas ratios of 0.2:1.0 and 0.4:1.0 usually recovered the correct phylogeny more often than use of the slowly evolving characters alone. For ease of interpretation, we show only the results for the fast : slow weighting ratios 0:1.0, 1.0:0, 1.0:1.0, and 0.2:1.0; 0.2:1.0 gave the correct estimate most often. For the rapidly evolving data set, branch lengths were 60% expected internodal change; for the slowly evolving data set, branch lengths were 35% expected internodal change. Each data point represents the average of 1,000 simulated phylogenies. See Bull et al. and Huelsenbeck and Hillis (1993) for further details of the simulations.

of characters in which one set yielded trees with highly unequal branch lengths. But these examples do not involve weaknesses unique to data combination; rather, they are cases in which the fundamental assumptions of parsimony analysis are violated. In the worst case scenario, such violations could include several data sets, causing the results of separate analyses to converge on the same wrong answer. For instance, problems of nonindependence could extend across multiple partitions of the data (e.g., possible convergent evolution of biochemical, physiological, morphological, and behavioral traits correlated with homeothermy in birds and mammals), as could problems of hybridization (e.g., in morphology, chromosomes, proteins, and mitochondrial DNA in fishes; Smith, 1992) and unequal branch lengths (e.g., because of sampling distantly related taxa; Swofford and Olsen, 1990).

However, if violations are restricted to one or a few data sets, then giving less weight to the sets of characters suspected of being misleading (as advocated by Swof-

ford and Olsen, 1990) or addition of enough characters from other data sets should result in estimation of the correct phylogeny by a combined analysis. The example of lateral gene transfer (Dykhuizen and Green, 1991) and the simulations that used an inconsistent data set (Bull et al.'s fig. 4) appear to be cases in which downweighting characters in one set or adding characters from other data sets should lead to recovery of the true phylogeny. Because lateral transfer normally will involve only one gene or a linked genic array, inclusion of additional data in a single analysis should diminish the misleading effects of the transferred gene(s). Moreover, if the transfer event is relatively old, the transferred gene(s) may still contribute phylogenetic signal that is consistent with the organismal phylogeny.

An inconsistent data set might also be treated by application of a correction for multiple hits (e.g., nonlinear transformation of the data; Steel et al., 1993). With such a correction scheme, an inconsistent data set could positively contribute to phylogeny estimation rather than simply having its negative impact reduced by weighting (J. Huelsenbeck, pers. comm.). If this correction were possible in the context of a combined analysis, we would consider it a form of weighting.

Bull et al. (1993), de Queiroz (1993), and Swofford (1991) have argued that use of combined analysis alone will obscure some patterns of congruent and discordant characters (and thus possible violations of assumptions) that can be discovered using separate analyses of data set partitions. Although this is true, it also is true that proponents of the combined approach almost always perform separate analyses of subsets of their data in addition to combined analyses (e.g., Miyamoto, 1983; Kluge, 1989; Crother et al., 1992; Lee et al., 1992; Hillis et al., 1993; Wiens and Reeder, unpubl. manuscript). Proponents of character congruence have argued that analysis of the combined data gives the best estimate of phylogeny, not that separate analyses should never be performed. Furthermore, the prior agreement approach might prevent exploration of patterns of incongruence among other possible partitions of the total available data, because creation of new partitions would require combination of characters from partitions already determined to be uncombinable. Because many possible partitions can be equally justifiable for a given set of characters, this limitation is a serious concern.

We see the prior agreement approach as far less conducive to data exploration than is the character congruence approach (as it is actually practiced). Empirical studies have shown that in trees based on combined data, relationships can appear that are absent in the shortest trees from the separately analyzed partitions. A nonexhaustive survey of the literature (Table 1) indicates that combined analyses generate trees that are incongruent with each of those from the separately analyzed data sets in more than half the cases. Thus, combination of data can allow discovery of relationships (and therefore sets of congruent and discordant characters) that would have been missed had the data sets only been analyzed separately. Of course, the novel relationships discovered by combining data could be wrong. But unless the data are somehow divided cleanly into "good" and "bad" sets of characters (e.g., rapidly and slowly evolving characters), Bull et al.'s simulations show that accuracy increases (up to a point) with increasing numbers of characters (their figs. 3, 4). Thus, data combination seems likely to increase accuracy by maximizing the number of characters used in a single analysis (unless the data are inconsistent).

Limitations of the Prior Agreement Approach

Suppose that one followed the prior agreement approach, partitioned the available data, and obtained significantly different trees (or simply trees that were well supported and in disagreement). Bull et al. suggested trying to identify ("know") a cause of heterogeneity (p. 385, fig. 1), and if this were possible, one could then revise the reconstruction model. The only means of revision that they suggested was differ-

TABLE 1. Are trees from separate analyses of data sets congruent with those from combined analyses? Results of a literature survey of cases in which authors performed both separate and combined analyses of sets of characters.

Organism	Data sets	Combined tree(s)[a]	Reference
Escherichia coli strains	6-phosphogluconate dehydrogenase (*gnd*) gene/tryptophan B gene	*gnd* gene	de Queiroz (1993)
Plants (Asteraceae)	nonmolecular/chloroplast (cp) DNA	cpDNA	Doyle (1992)
Plants (Solanaceae)	cpDNA restriction sites/*ndh*F gene/ribulose bisphosphate carboxylase-oxygenase (*rbc*L) gene	unique	Olmstead and Sweere (unpubl. data)
Plants (Solanaceae)	*ndh*F gene/*rbc*L gene	unique	Olmstead and Sweere (unpubl. data)
Plants (Solanaceae)	*ndh*F/cpDNA restriction sites	cpDNA restriction sites and unique	Olmstead and Sweere (unpubl. data)
Plants (Solanaceae)	*rbc*L/cpDNA restriction sites	cpDNA restriction sites and unique	Olmstead and Sweere (unpubl. data)
Dwarf dandelions (*Krigia*)	morphology/ribosomal (r) DNA/ITS[b]/cpDNA	unique	Kim and Jansen (1994)
Arthropods	morphology/18S rDNA/ubiquitin gene	morphology	Wheeler et al. (1993)
Arthropods	18S rDNA/ubiquitin gene	unique	Wheeler et al. (1993)
Butterflies (*Amauris*)	morphology/male scent gland compounds	morphology	Vane-Wright et al. (1992)
Heliconiine butterflies	morphology/rDNA restriction sites	unique	Lee et al. (1992)
Vertebrates	28S rRNA (stems)/28S rRNA (loops)	28S rRNA (stems)	Dixon and Hillis (1993)
Atherinid fishes (*Menidia*)	morphology/allozymes	unique	Mickevich and Johnson (1976)
Ambystomatid salamanders	morphology/allozymes	unique	Shaffer et al. (1991)
Frogs	morphology/28S rDNA	unique	Hillis et al. (1993)
Leptodactylid frogs (*Eleutherodactylus*)	morphology/allozymes/karyology	morphology	Miyamoto (1983)
Mammals	morphology + restriction sites/mitochondrial (mt) coenzyme III and epsilon globin DNA sequences + alpha and beta hemoglobin and alpha crystallin amino acid sequences	unique	Ammerman Dixon (1993)
Pecoran mammals	mt 12S rRNA/mt 16S rRNA/mt cytochromome *c* oxidase subunit II	mt 16S rRNA	Miyamoto et al. (1994)
Kinosternid turtles	morphology/allozymes[c]	unique	Iverson (1991)
Phrynosomatid lizards	morphology/mt 12S and 16S rRNA	unique	Wiens and Reeder (unpubl. manuscript)
Xantusiid lizards	mt 12S rRNA/cytochrome *b* gene	mt 12S rRNA	Hedges et al. (1991)
Boine snakes (*Epicrates*)	morphology/scent gland lipids	unique	Kluge (1989)
Rattlesnakes (*Crotalus*)	morphology/allozymes	morphology	Barker (1992)
Palm pitvipers (*Bothriechis*)	morphology/allozymes	both	Crother et al. (1992)
Birds	morphology/rDNA/alpha crystallin A amino acid sequences	morphology/alpha crystallin A	Cracraft and Mindell (1989)

[a] Indicates whether the tree(s) from the combined analysis is consistent with trees from separate analyses of any of those data sets or whether it has a topology not found in separate analyses of the data sets (i.e., a unique topology). Sequence data sets are indicated by the name of the molecule or gene.

[b] ITS = internal transcribed spacer of nuclear rDNA.

[c] For the allozyme data, coding locus as the character; coding allele as the character also yields a unique topology when combined with morphological data.

ential weighting of characters (which is meaningful only in the context of a combined analysis).

In cases in which the cause of heterogeneity cannot be identified, Bull et al. offered no suggestions as to how to proceed, other than to entertain the alternative trees as possible solutions (p. 385). De Queiroz recommended use of consensus trees when separate analyses of data sets yield strongly supported alternative phylogenies. In either case, one can proceed no further unless additional criteria are instituted regarding the number of data sets that must agree, whether the "homogeneous" partitions can be combined, whether new data can be added to existing partitions, and so on. Otherwise, one will be left with conflicting hypotheses of relationships that no amount of new data can overturn; thus, these hypotheses will effectively be untestable.

Bull et al. took the position that "it is better to obtain one right answer and one wrong answer from separate analyses than to get a single wrong answer in a combined analysis" (p. 385). If these are the only possible results, then obtaining two alternative trees may indeed be preferable. But these are not the only possible outcomes. In the real world, one will not know (1) whether the correct tree is among the alternative answers, (2) which alternative tree is the correct one, and (3) whether the tree that results from the combined analysis is correct. All the trees that result from separate analyses may be incorrect, whereas a combined analysis may yield the correct tree. Furthermore, the same incorrect groups may appear in the trees that result from the separate analyses (e.g., Barrett et al., 1991). If this is the case, then a consensus approach (as advocated by de Queiroz) would simply reinforce confidence in an incorrect phylogenetic conclusion. One can even imagine a situation (analogous to that of Barrett et al., 1991) in which nonparametric bootstrapping (=bootstrapping sensu Felsenstein, 1985) of partitioned data sets shows strong support for conflicting clades in the alternative trees and strong support for the same incorrect clade, whereas parsimony analysis of the combined data would yield the correct tree (see Fig. 2 for an example).

A related problem of the prior agreement approach is that the tests of heterogeneity among trees that Bull et al. and de Queiroz suggested, such as Faith's (1991) T-PTP test and nonparametric bootstrapping, respectively, measure only degree of support for particular clades within data sets. Thus, one might have a large number of independent characters that support a particular (correct) clade in the analysis of one data partition and a much smaller number of characters that support an alternative (incorrect) clade in the analysis of another partition. Even though there is overwhelming support for the clade supported by the larger number of characters, one would be prevented from combining the data (and recovering the single correct phylogeny) because of the initial determination of heterogeneity (see example in Fig. 3).

Even if the correct tree is obtained more often by separate analyses than by combination of data sets, we still question the value of the prior agreement approach. Bull et al. simulated such a situation, but the results shown in their figure 3 reveal very little difference between the curve that represents the probability of finding the correct tree using only slowly evolving characters and the curve derived by combining rapidly and slowly evolving characters (even without differential weighting of characters). This similarity was evident even when the rapidly evolving characters outnumbered the slowly evolving characters by a ratio of 4:1 (their fig. 3b). One could argue that the different trees obtained by separate analyses in this example might not be found to be "significantly heterogeneous." In such cases, one would combine the data anyway, and this set of simulations still would show no advantage of the prior agreement approach.

Consider the case for 100 characters, based on Bull et al.'s simulation (their fig. 3a). If one were to analyze only the rapidly evolving data set, the chance of obtaining the correct tree would be approximately 40%. If one were to analyze only the slowly evolving data set, the chance of obtaining

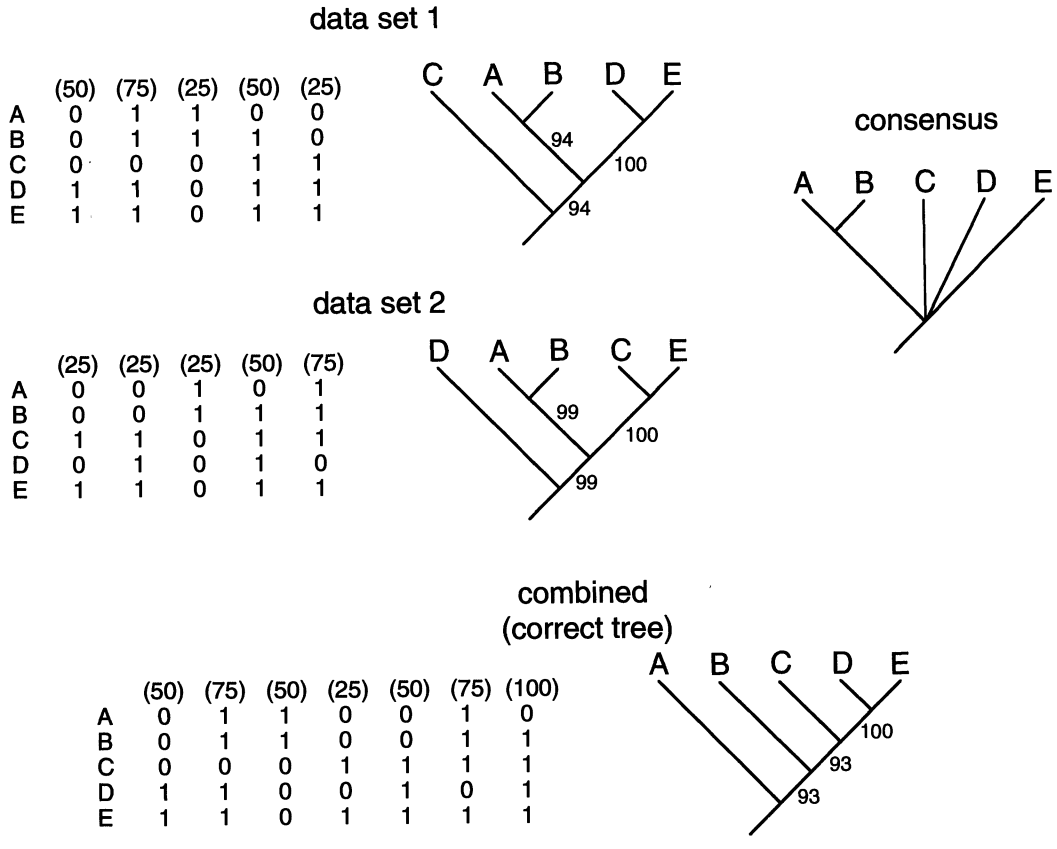

FIGURE 2. A hypothetical case in which separate parsimony analyses of two data sets show strong support for conflicting relationships and strong support for the same incorrect relationships (after Barrett et al., 1991). A strict consensus tree resolves only the incorrect relationship (A + B), whereas a combined analysis recovers the correct tree. Numbers in parentheses above each column in the data matrices indicate the number of characters with a particular distribution of character states among taxa. Numbers on the trees indicate the number of times the clade appeared in 100 nonparametric bootstrap pseudoreplicates. Analyses were performed using PAUP 3.0s (Swofford, 1990). Characters in different data sets were weighted equally in the separate and combined analyses.

the correct tree would be roughly 85%. If one combined the data sets, the chance of obtaining the correct tree would be about 78%, just slightly less than if the slowly evolving characters were analyzed alone. Thus, in about 60% of the cases in which the data sets were treated separately, one would be forced by the criteria of Bull et al. to give equal consideration to both an incorrect phylogeny and a correct one (or to two incorrect trees). The alternative would be to combine the data sets and enjoy a relatively high probability (about 78%) of estimating the single correct tree. We do not believe that one should strive to obtain a single most-parsimonious tree at any cost. However, if the cost (in terms of the probability of estimating the correct tree) is small, as in the example above, there is little to be lost and much to be gained by combination of data.

PROBLEMS OF PARTITIONING DATA

Given a set of characters for phylogenetic analysis, many different partitions are possible, and the choice of appropriate partitions is difficult at best. The application of any given criterion in partitioning prevents the process from being truly arbitrary, but the logical basis for choice of one

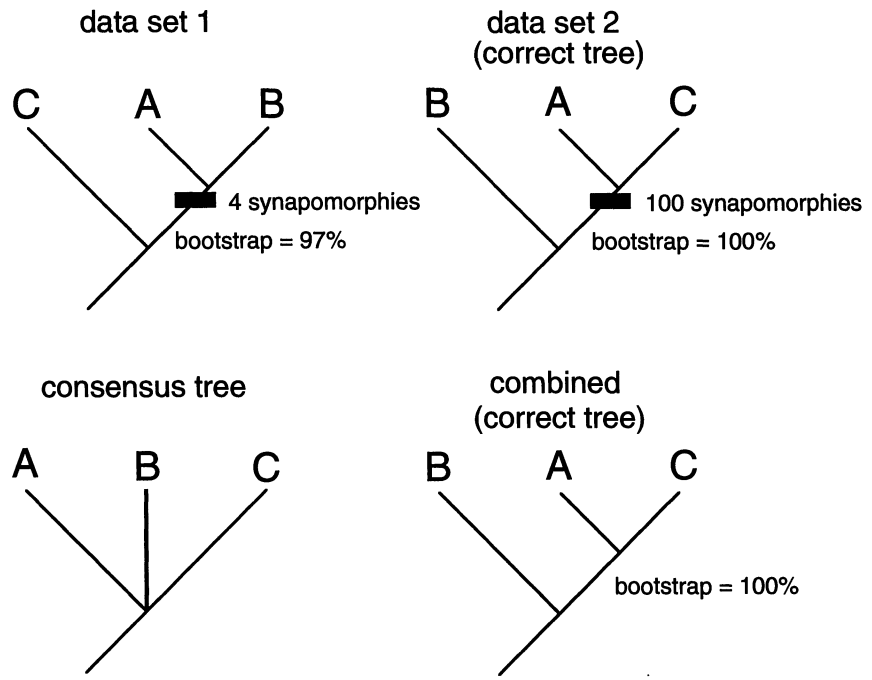

FIGURE 3. A hypothetical example in which two data sets show strong support for conflicting relationships (as determined by nonparametric bootstrapping). The prior agreement approach (as advocated by de Queiroz, 1993) would require that these data sets be kept separate and the relationships remain unresolved (in a consensus tree). Data set 2 contains overwhelming support for the correct phylogeny, which is recovered if the data are combined. Analyses were performed using PAUP 3.0s (Swofford, 1990). Characters in different data sets were weighted equally in the separate and combined analyses.

partitioning scheme over another is unclear. A given character usually can be assigned to any one of many partitions. For example, the presence of external gills in a salamander might equally well be classified as a larval (versus adult), cranial (versus postcranial), or soft anatomical (versus hard anatomical) character. Each of these partitions would place this character into a data set with different characters.

The most valuable criterion for partitioning of characters is the relative evidential value of the characters in the context of all the data, where evidential value is defined as the probability that the distribution of character states among taxa reflects the organismal phylogeny. However, characters that should be similarly weighted are likely to be intermingled among many traditional divisions of data. For example, there are characters that are likely to have limited value in both morphological (e.g., characters influenced strongly by size; Kluge, 1989) and molecular (e.g., third codon positions) data.

CHARACTER WEIGHTING

Although we strongly advocate differential weighting as a means of integrating diverse data sets, we acknowledge that one does not know exactly what weights are appropriate any more than one knows what the true phylogeny is. However, there are many sources of information available that can be used to estimate the appropriate weights, including probabilistic arguments (e.g., loss versus gain of restriction sites, De Bry and Slade, 1986), information from other studies (e.g., transitions generally occur more frequently than transversions, Brown et al., 1982), the data themselves (e.g., combinatorial weights, Wheeler, 1990; expected to observed ratio weighting, Knight and Mindell, 1993;

weighting for compensatory changes in rDNA, Dixon and Hillis, 1993), or perhaps even the congruence of characters on the tree(s) derived from phylogenetic analysis of the data (e.g., successive approximations; Farris, 1969). Although Bull et al. stated that different partitions "yield direct insight to different processes and mechanisms" (p. 394), the discovery of (significantly) different trees based on data partitions alone reveals nothing about the relative value of the different sets of characters in phylogeny reconstruction.

CONCLUSIONS

Integration of diverse data is a highly contentious issue in modern systematics. Bull et al. (1993) and de Queiroz (1993) suggested novel approaches to this problem that raise important questions. They advocated separate analyses of subsets of the total available data (which can be partitioned any number of ways), and they allowed combination of the data only if the trees that result from the separate analyses are not in disagreement (according to the chosen test). However, this approach can result in alternative hypotheses for a group of taxa (all of which may be incorrect) that may be untestable (if they cannot be overturned by additional characters) and that may hinder further exploration of the data. Furthermore, Bull et al.'s computer simulations showed that there are likely to be cases in which separate analyses lead to different alternative trees (with no basis for choosing among them), when combination is almost as likely to result in the correct tree being estimated.

We advocate an approach to phylogenetic analysis of diverse data that involves differential character weighting (to accommodate different evolutionary processes) carried out in the context of the combined (total) data. This approach offers the opportunity to simultaneously incorporate both the growing wealth of character data and the increasing knowledge of the processes of character evolution.

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