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CONSISTENCY INDICES AND RANDOM DATA

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Abstract.—This study was undertaken to determine the range of consistency index (CI) values obtainable from random data sets. We generated multiple random data matrices for each of 49 different matrix sizes ranging from 5 taxa and 4 (binary) characters to 49 taxa and 124 characters. The CI of the minimum-length tree(s) was calculated for each. CIs decreased in a monotonic, nonlinear fashion with addition of either taxa or characters. The influence of addition of taxa was far greater than that of addition of characters, and an interaction effect was recognized. The general curvilinear relation we found between CIs and number of taxa is consistent with results obtained by other authors, but our random data CIs were lower than those of other studies. Mean random CIs varied from 0.70 for the smallest data sets to 0.072 for the largest. Maximum random CIs reached 0.80. A regression through means of random CIs against number of taxa was calculated with a 95% confidence interval. This CI_{random} is the minimum value that real data sets should exceed to be considered to contain phylogenetic information. The CIs of real data sets can be adjusted with the CI_{random} , and these values are found to meet current criteria for adequate measures of homoplasy. However, the homoplasy indices that are uncorrelated with taxa are also insensitive to internal data set structure, and no current index is adequate for comparison of homoplasy among data sets. [Consistency index; random data; homoplasy comparison; phylogenetic information content.]

The consistency index (CI) was introduced by Kluge and Farris (1969) to measure the degree to which a "phyletic tree" or cladogram deviates from a perfect fit to the data. It is simply the minimum number of steps required to explain a given data set divided by the actual number of steps that is observed on a resulting tree. This ratio ranges in value from near zero to one, with higher values indicative of a better fit of the cladogram to the data. In essence, the CI provides a measure of the homoplasy exhibited by a cladogram; low CIs indicate high levels of homoplasy and high CIs indicate low levels of homoplasy. The amount of homoplasy exhibited by a cladogram is usually considered inversely proportional to the confidence that an investigator will have in both the tree and the data set from which it was derived (but see Sanderson and Donoghue, 1989). Because the level of homoplasy is such an important statistic, numerous additional measures have since been produced, including the *F*-ratio (Farris, 1972), the *D* measure (Brooks et al., 1986), the homoplasy excess ratio (Archie, 1989b) or its apparent equiv-

alent the retention index (Farris, 1989a), and the homoplasy slope ratio (Meier et al., 1991). Most of these authors have introduced their measures in response to perceived inadequacies of previous ones, particularly the CI. Archie (1989a, 1989b) was especially concerned by the significant negative correlation of the CI with number of taxa, which suggested to him that it is not suitable for comparing the relative merits of one cladogram over another. Similar concerns stimulated other workers to explore the inherent properties of the CI (Sanderson and Donoghue, 1989; Meier et al., 1991).

Despite its many detractors, the CI remains the most widely used measure of homoplasy and of confidence an investigator might place in a given data set. Its popularity stems from both its simple calculation and its intuitive appeal. It is likely that the CI will continue to be used by phylogenetic systematists as a convenient tool for evaluating data sets and their resulting cladograms. But when should an investigator lose confidence in a cladogram because of a particular CI value?

When does a CI value suggest that a data set holds little or no phylogenetic information? We felt that a start in answering these questions could be made by examining the CI values generated when random data sets are used to build cladograms. Comparing CIs of cladograms from random data sets with CIs for actual data sets of similar size should provide at least a minimum level of acceptance and confidence.

This paper presents our findings regarding CI values obtained from random data sets and compares them with values for actual data from the literature. We examine the criteria implemented by Archie (1989a) and Meier et al. (1991) to assess the performance of homoplasy indices, and find that some of these can be met by a simple rescaling of the CI using the relationship of the random data CIs with number of taxa. We do not introduce this rescaling as another measure of homoplasy, but use it to investigate the practicality of comparing homoplasy levels among data sets.

MATERIALS AND METHODS

A program (available on request) was written in GW-BASIC to generate binary-state data sets with equal probability of 0 or 1 for each character state for use in cladistic analysis. To eliminate symplesiomorphies and autapomorphies from CI calculations, data sets with characters consisting of all 0's, all 1's, or only a single 1 were discarded, as were data sets with any taxon exhibiting the plesiomorphic state (0) for all characters. Thirty replicate data sets were generated for each of 49 taxon-by-character combinations (5-49 taxa and 4-124 characters), for a total of 1,470 data sets. The data sets were generated in eight strings based on the following taxon-character relationship:

$$n_i \text{ by } xn_i + (n_i - 1),$$

where n is number of taxa of the i th string and x is a multiplication factor chosen for each string such that for $x = 0$ the number of characters is $n - 1$ (Fig. 1). This is the base number of characters because it is the

minimum number required to permit complete resolution of a cladogram involving n taxa. Only three data set sizes were run for the smallest number of taxa used (five). This limitation is the result of the limited number of possible character-state permutations for low numbers of taxa. The likelihood of inadmissible character strings appearing (all 0, all 1, or only one 1) is very high, making it increasingly difficult to generate large numbers of random data sets for few taxa and large numbers of characters.

Cladistic analyses were conducted using PAUP (Phylogenetic Analysis Using Parsimony) version 2.4.1, written by D. Swofford (Illinois Natural History Survey). The branch-and-bound option of PAUP was used only for the smallest data sets (five taxa). All other data sets were analyzed using the global branch swapping option (SWAP=GLOBAL) to estimate the shortest tree(s). Characters of all data sets were polarized by including a hypothetical ancestor (all 0's).

Statistical analysis was carried out using PC-SAS, release 6.03 (SAS Institute, 1988). All statistical tests were carried out using logged variates to reduce the correlation of variance with mean CI (Sokal and Rohlf, 1981). A fixed-effects analysis of variance was performed to assess the importance of numbers of taxa and characters on CI values. In addition, we carried out regression analysis of CI on number of taxa. Analysis of covariance (ANCOVA) was used to determine whether the effects of varying numbers of characters on CI were similar over the full range of numbers of taxa. The ANCOVA can be visualized as a comparison of a series of regressions of CI on number of characters, with one regression line for each level of taxa. If the effect of characters on CI is the same for all numbers of taxa, the slopes and intercepts of the regression lines will be the same; otherwise, either the slopes or the intercepts will differ.

Analysis of covariance was used to compare CIs from our randomly generated data sets to CIs of actual data sets analyzed by Archie (1989a) and Sanderson and Dono-

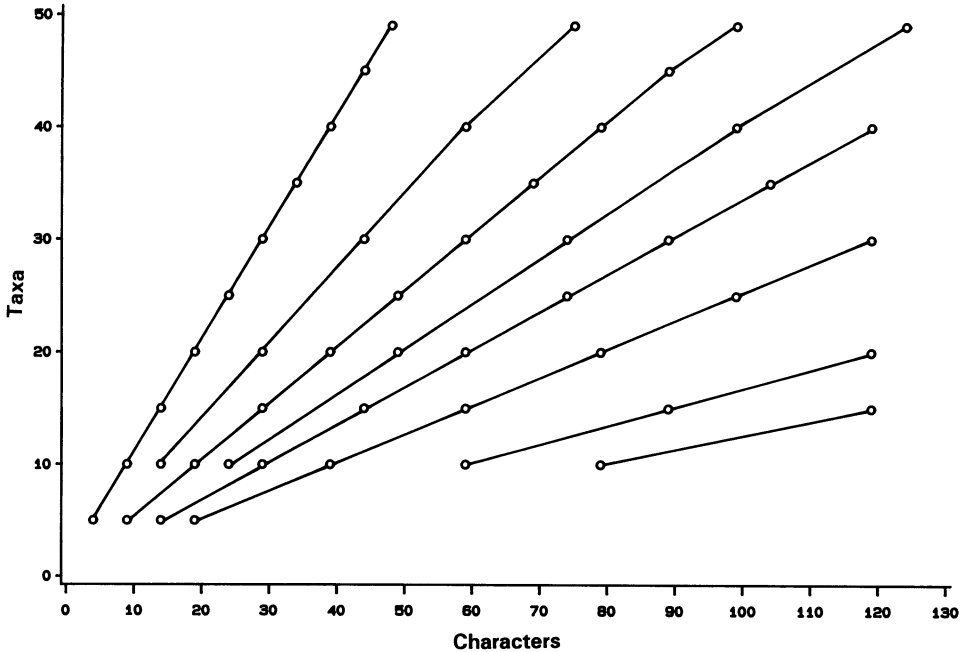


FIGURE 1. Distribution of 49 taxon-by-character combinations, for each of which 30 data sets were generated.

ghue (1989) and to CIs of data sets randomized by Archie (1989a).

RESULTS

Consistency index values for randomly generated data sets decreased with increasing numbers of either taxa or characters (Fig. 2). Mean CI ranged from 0.700 for the smallest data set (5 taxa \times 4 characters) to 0.072 for the largest data set (49 taxa \times 124 characters), with standard deviation decreasing monotonically with decreasing CI (Table 1). Figure 2 clearly shows that the largest decrements in CI were observed for the smallest numbers of taxa or characters. For example, reducing data set size from 10 to 5 taxa will have a greater effect on the CI than reducing the data set size from 50 to 45 taxa. Maximum CI exceeded 0.3 for all data sets with 10 or fewer taxa, attaining 0.8 for the smallest data set (5 taxa \times 4 characters) (Table 1). Tree topologies for all data sets yielding maximum CI values were fully resolved.

Analysis of variance showed main and interaction effects of numbers of taxa and characters on CI to be significant (Table 2).

Further analyses focused on the effects of number of taxa because the variance in CI explained by this main effect was 98.54%, whereas only 1.17% of variance was explained by number of characters. Duncan's comparison of means showed CIs for all numbers of taxa to be significantly different from one another (Table 3).

Regression analysis of random data CIs on number of taxa produced the relationship (Fig. 3)

$$CI = 2.9370 \times n^{-0.9339} \quad (r^2 = 0.9829), \quad (1)$$

where n is number of taxa.

Results of the ANCOVA (Table 4) show that (1) the slopes of the regressions of random CIs on characters are significantly different from 0 (a significant character effect) and (2) the slopes of the regressions differ between number of taxa (a significant interaction effect). This indicates that the number of characters does have a small, but significant, effect on random CI, and that this effect varies depending on the number of taxa involved (Fig. 4).

Comparison of CIs from random data sets and CIs from data sets of real taxa (Fig. 5)

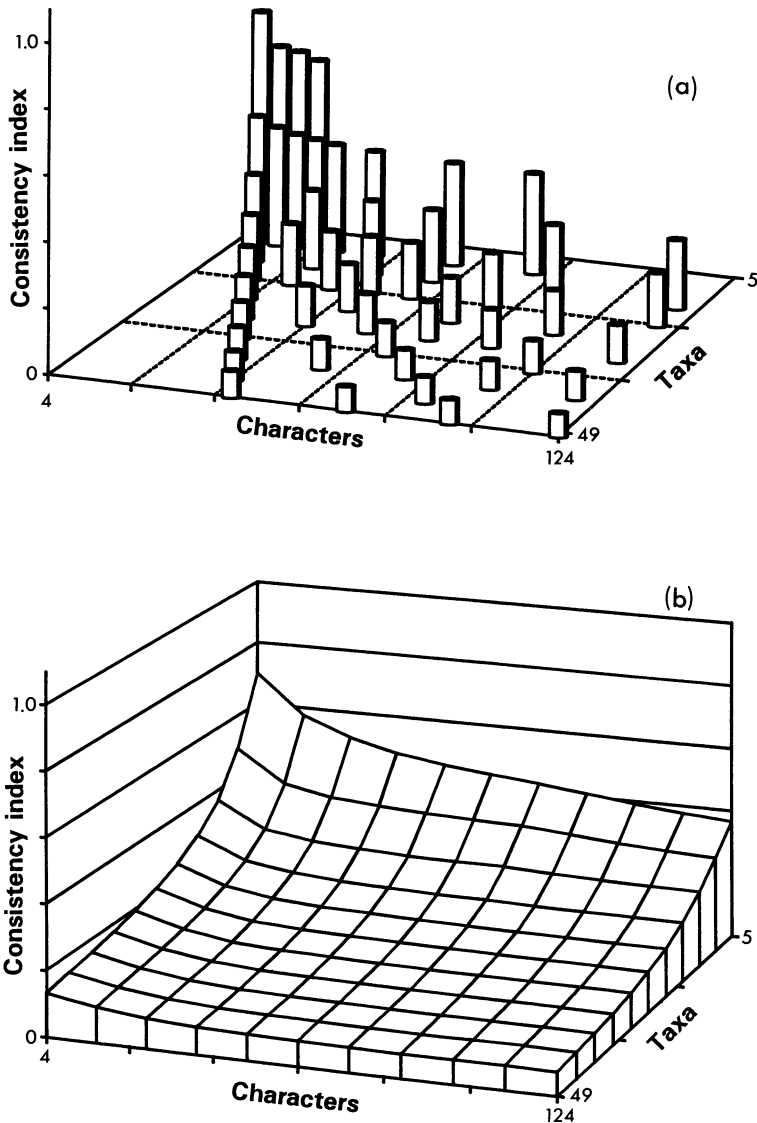


FIGURE 2. (a) Effects of number of characters and number of taxa on mean CI for the 49 taxon-by-character combinations. (b) Spline interpolation of mean CI based on 49 taxon-by-character combinations.

shows that the real CIs are consistently higher than our mean random CIs. ANCOVA shows that CIs of real data summarized by Archie (1989a) and Sanderson and Donoghue (1989) (Fig. 6) and Archie's (1989a) randomized data (Fig. 7) are significantly different from CIs of our random data. Regression analysis of CI on number of taxa for real (Equation 2) and randomized (Equation 3) data produces the following relationships:

$$CI = 2.123 \times n^{-0.485} \quad (r^2 = 0.5907); \quad (2)$$

$$CI = 3.177 \times n^{-0.787} \quad (r^2 = 0.9066). \quad (3)$$

DISCUSSION

The initial goal of this study was to determine the range of CIs that can be obtained for random data sets of a given size, irrespective of topology. Since we began, several papers have been published ad-

TABLE 1. Mean \pm SD, minimum, and maximum CI values for each combination of taxa and characters (30 data sets for each).

Number of taxa	Number of characters	Mean \pm SD	Minimum	Maximum
5	4	0.700 \pm 0.0705	0.571	0.800
5	9	0.592 \pm 0.0302	0.529	0.643
5	14	0.581 \pm 0.0418	0.538	0.737
5	19	0.559 \pm 0.0253	0.514	0.613
10	9	0.411 \pm 0.0287	0.360	0.474
10	14	0.383 \pm 0.0211	0.350	0.438
10	19	0.366 \pm 0.0194	0.339	0.404
10	24	0.356 \pm 0.0134	0.329	0.387
10	29	0.346 \pm 0.0147	0.326	0.392
10	39	0.338 \pm 0.0102	0.315	0.358
10	59	0.327 \pm 0.0096	0.312	0.349
10	79	0.321 \pm 0.0075	0.306	0.338
15	14	0.280 \pm 0.0143	0.259	0.311
15	29	0.249 \pm 0.0115	0.232	0.271
15	44	0.236 \pm 0.0063	0.221	0.251
15	59	0.228 \pm 0.0042	0.221	0.237
15	89	0.223 \pm 0.0044	0.216	0.231
15	119	0.218 \pm 0.0030	0.215	0.226
20	19	0.208 \pm 0.0078	0.188	0.221
20	29	0.194 \pm 0.0070	0.181	0.212
20	39	0.184 \pm 0.0039	0.176	0.193
20	49	0.181 \pm 0.0046	0.170	0.191
20	59	0.176 \pm 0.0037	0.168	0.183
20	79	0.171 \pm 0.0023	0.167	0.177
20	119	0.167 \pm 0.0022	0.164	0.172
25	24	0.166 \pm 0.0037	0.158	0.173
25	49	0.148 \pm 0.0026	0.143	0.154
25	74	0.141 \pm 0.0031	0.137	0.152
25	99	0.138 \pm 0.0021	0.135	0.142
30	29	0.135 \pm 0.0027	0.129	0.140
30	44	0.127 \pm 0.0030	0.123	0.138
30	59	0.122 \pm 0.0019	0.119	0.128
30	74	0.118 \pm 0.0017	0.115	0.122
30	89	0.117 \pm 0.0016	0.115	0.120
30	119	0.115 \pm 0.0012	0.113	0.118
35	34	0.115 \pm 0.0019	0.111	0.118
35	69	0.104 \pm 0.0011	0.102	0.107
35	104	0.100 \pm 0.0007	0.099	0.101
40	39	0.099 \pm 0.0018	0.095	0.103
40	59	0.094 \pm 0.0012	0.092	0.096
40	79	0.090 \pm 0.0008	0.089	0.092
40	99	0.089 \pm 0.0007	0.087	0.090
40	119	0.087 \pm 0.0009	0.086	0.089
45	44	0.088 \pm 0.0011	0.086	0.090
45	89	0.080 \pm 0.0007	0.078	0.081
49	48	0.080 \pm 0.0011	0.078	0.082
49	75	0.075 \pm 0.0008	0.074	0.077
49	99	0.073 \pm 0.0008	0.071	0.073
49	124	0.072 \pm 0.0006	0.072	0.075

addressing similar problems. Meier et al. (1991: their Table 1) presented CIs for random data sets of 4–10 taxa and 7–100 characters. They reported mean CIs and standard deviations that were similar to, but consistently higher than, those we present (Table 1). Unlike our procedure of data set generation, Meier et al. (1991) did not eliminate autapomorphies and symplesiomorphies from their random data sets before CIs were calculated. As pointed out by Brooks et al. (1986), inclusion of autapomorphies will artificially inflate CIs. Symplesiomorphies will also inflate CIs, as they are necessarily congruent with any tree topology produced by the remaining characters of the data matrix. We believe that our random data CI values provide a better comparison with CI values from data matrices of real taxa because they are consistent with accepted practice of CI calculation.

The random data CIs and their correlation with number of taxa (Equation 1; Fig. 7) are significantly lower than the CIs produced by Archie's (1989a) randomized real data sets (Equation 3; Fig. 7). The procedure used by Archie (1989a, 1989b) "scrambles" real data sets by repeatedly randomizing the distributions of the character states across taxa. This constrains the degree of randomness that a given data set size can exhibit. The CIs of trees generated from randomized data sets that preserve the character-state frequencies of the real data will be higher than CIs generated by random data. Meier et al. (1991) pointed out that this observation concurs with the theoretical expectations outlined by Meacham (1981, 1984) and Sanderson and Donoghue (1989:1784), where "data sets that include a large proportion of characters with highly unequal distributions of states will tend to have higher CIs than those in which most characters have nearly equal distributions among the taxa."

Work conducted by previous investigators (Archie, 1989a, 1989b, 1990; Farris, 1989a, 1989b; Sanderson and Donoghue, 1989; Meier et al., 1991), together with the results from the current study, has raised doubts regarding the validity of the CI and

TABLE 2. Analysis of variance, fixed-effects model, for the main effects number of taxa and number of characters, and their interaction effect, on logged CI of randomly generated data sets.

Source	df	Sum of squares	Mean square	F	Pr > F
Taxa	9	104.243	11.583	58,907.81	0.0001
Characters	19	1.242	0.065	332.55	0.0001
Interaction	20	0.023	0.001	5.94	0.0001
Error	1,421	0.279	0.0002		
Total	1,469	105.787			

% variance explained by Taxa = 98.54%
 % variance explained by Characters = 1.17%

its modifications/alternatives as overall measures of homoplasy, and the use of these measures for comparing among data sets. It was not until the studies by Archie (1989a, 1989b) and Sanderson and Dono-

ghue (1989) that the intrinsic properties of the CI came under close scrutiny. Both of these authors recognized a strong inverse curvilinear relationship between CI and number of taxa. This relationship was con-

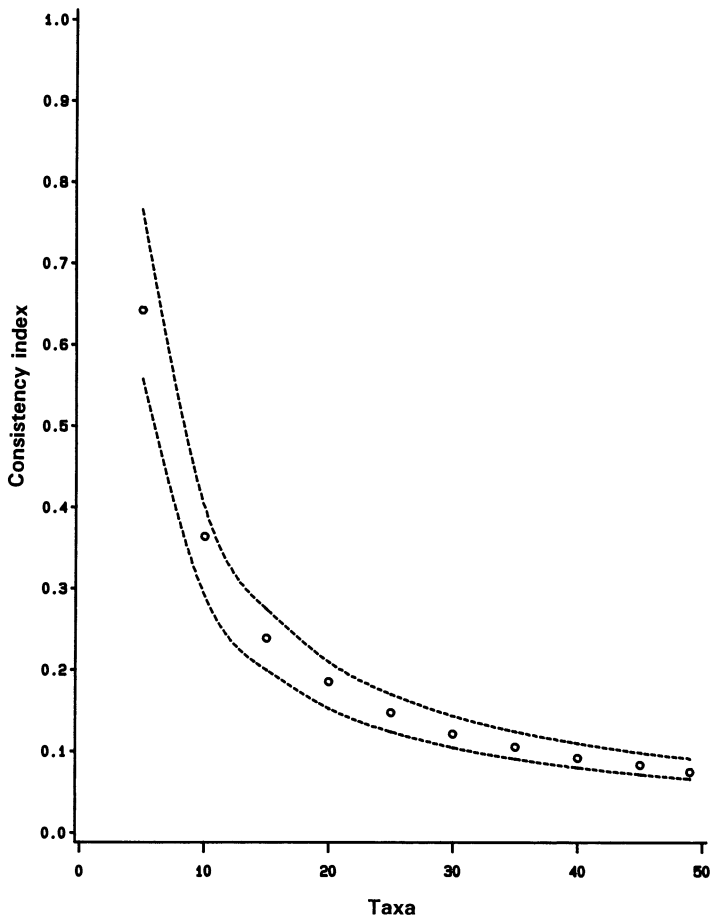


FIGURE 3. Mean (O) and 95% confidence intervals (---) of CI for 5-49 taxa.

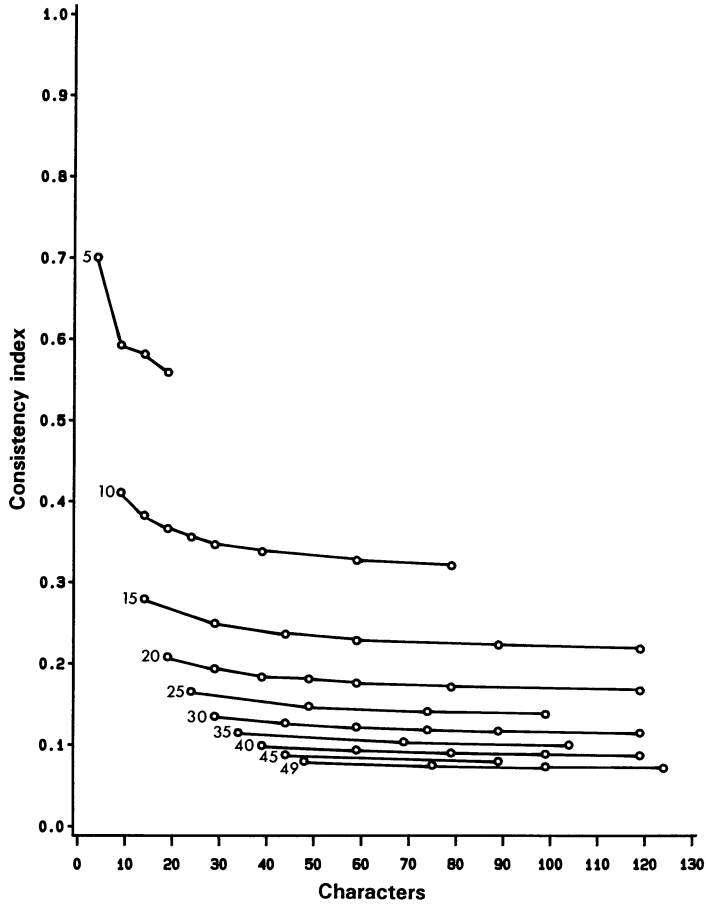


FIGURE 4. Effect of number of characters on mean CI for each number of taxa. Number of taxa labeled at left of plotted lines.

firmed by Meier et al. (1991) and is consistent with the taxon effect we have observed (Figs. 2, 3). Archie (1989a, 1989b) and Farris (1989a) interpreted this relationship as an artifact of the CI. This being the case, Archie (1989a) argued that any measure of homoplasy should depend on the degree of hierarchical correlation between the characters and not necessarily be correlated with number of taxa. Correlation with number of taxa (and number of characters) severely limits the use of the CI for comparison among data sets. Additionally, even for data with no phylogenetic information, the CI cannot achieve its lower limit of zero, reiterating its ineffectiveness for comparative purposes (Archie, 1989a).

TABLE 3. Influence of varying number of taxa on mean CI of randomly generated data sets. All means are significantly different ($P < 0.05$, Duncan's multiple-range test). Means are presented for untransformed variates.

Number of taxa	Number of replicates	Mean CI
5	120	0.608
10	240	0.356
15	180	0.239
20	210	0.183
25	120	0.148
30	180	0.122
35	90	0.106
40	150	0.092
45	60	0.083
49	120	0.075

TABLE 4. Analysis of covariance, using number of characters as covariate for the main effect number of taxa on logged CI of randomly generated data sets.

Source	df	Sum of squares	Mean square	F	Pr > F
Taxa	9	104.243	11.583	52,644.77	0.0001
Characters	1	1.219	1.219	5,541.21	0.0001
Interaction	9	0.007	0.001	3.51	0.0003
Error	1,450	0.319	0.0002		
Total	1,469	105.788			

It has been generally concluded that the CI can no longer be considered an appropriate measure of homoplasy. Farris (1989a) suggested a modification of the CI, resulting in the retention index and rescaled consistency index. Archie (1989a, 1989b) proposed abandonment of the CI and introduced the homoplasy excess ratio. He rejected Farris's (1989a) retention index and rescaled consistency index by claiming that they, like the CI, were correlated with

number of taxa and were not scaled from zero to one, although supporting evidence was not provided. Meier et al. (1991) have since shown that the retention index is indeed correlated with number of taxa. However, they also showed that this problem exists with Archie's homoplasy excess ratio. Farris (1991) concurred, additionally demonstrating that Archie's measure did not have a minimum of zero. Meier et al. (1991) presented the homoplasy slope ratio

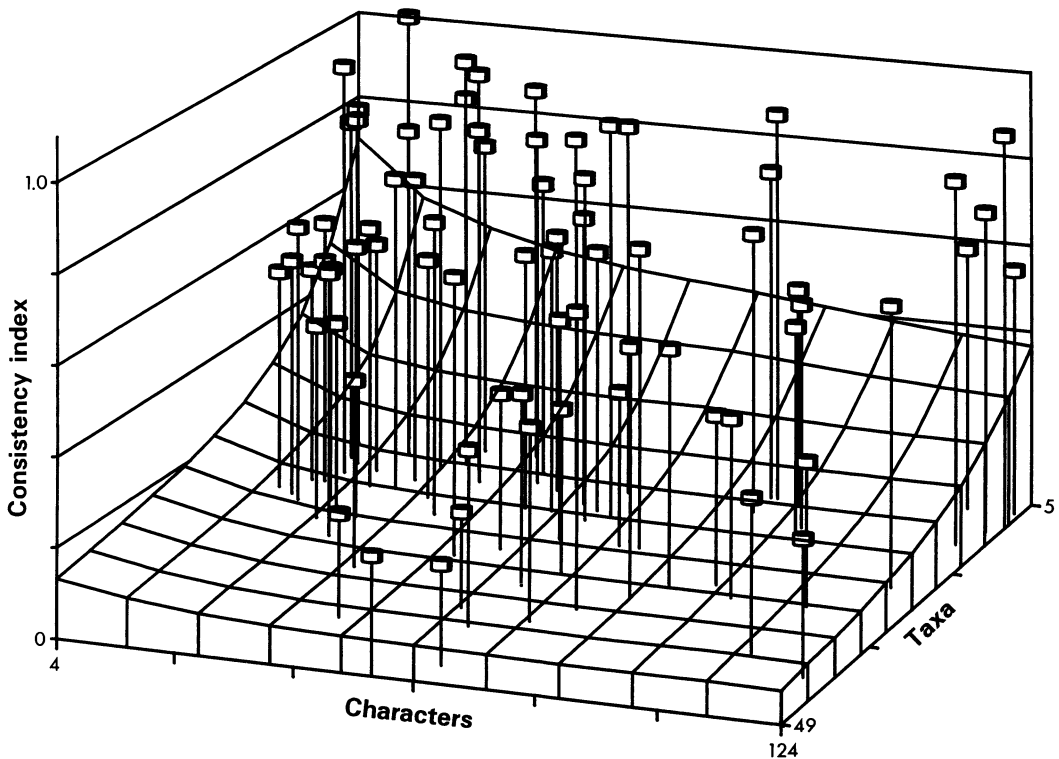


FIGURE 5. Comparison of CI values from published literature (Archie, 1989a; Sanderson and Donoghue, 1989) to spline-interpolated mean CIs for randomly generated data sets.

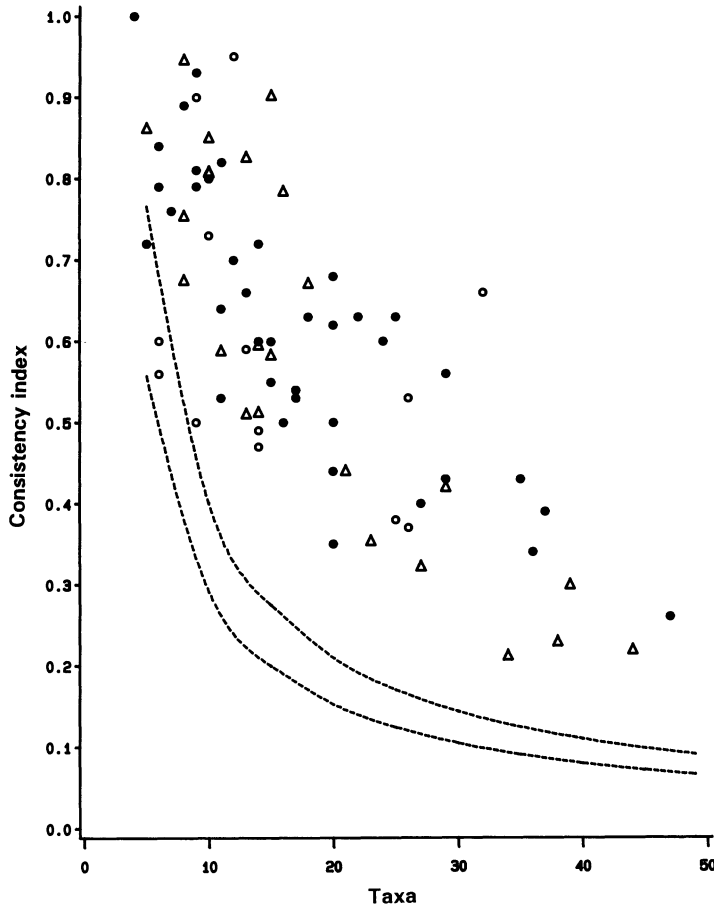


FIGURE 6. Comparison of CI values from published literature to 95% confidence limits of CIs from our random data sets, for 5–49 taxa. Δ , Archie (1989a); \circ , Sanderson and Donoghue (1989, molecular data); \bullet , Sanderson and Donoghue (1989, morphological data).

(HSR) as a measure of average homoplasy that is truly uncorrelated with number of taxa. We point out here that the HSR, which involves the CI or its equivalent in its calculation, will be affected by the inclusion of autapomorphies and/or symplesiomorphies. Such characters will artificially decrease the HSR, imply less homoplasy than might actually exist, and invalidate comparisons among data sets. Although the random homoplasy slopes calculated by Meier et al. (1991: their Table 2) have not taken autapomorphies or symplesiomorphies into account (i.e., values are too low), all HSRs will be similarly biased, and comparisons among real data sets remain valid.

We have taken a strictly empirical and more simplistic approach to the problem posed by CI correlation with number of taxa. Rather than abandon the CI, we recognize an absolute minimum CI value that must be exceeded for a data set to be considered phylogenetically informative. The mean minimum CI value is that obtained from our random data sets, estimated by

$$CI_{\text{random}} = 2.9370 \times n^{-0.9339}.$$

By comparing CIs for real data sets with those obtained from these random data, we obtain an impression of overall support for a particular data set. For instance, three data points in Figure 6 fall within the 95%

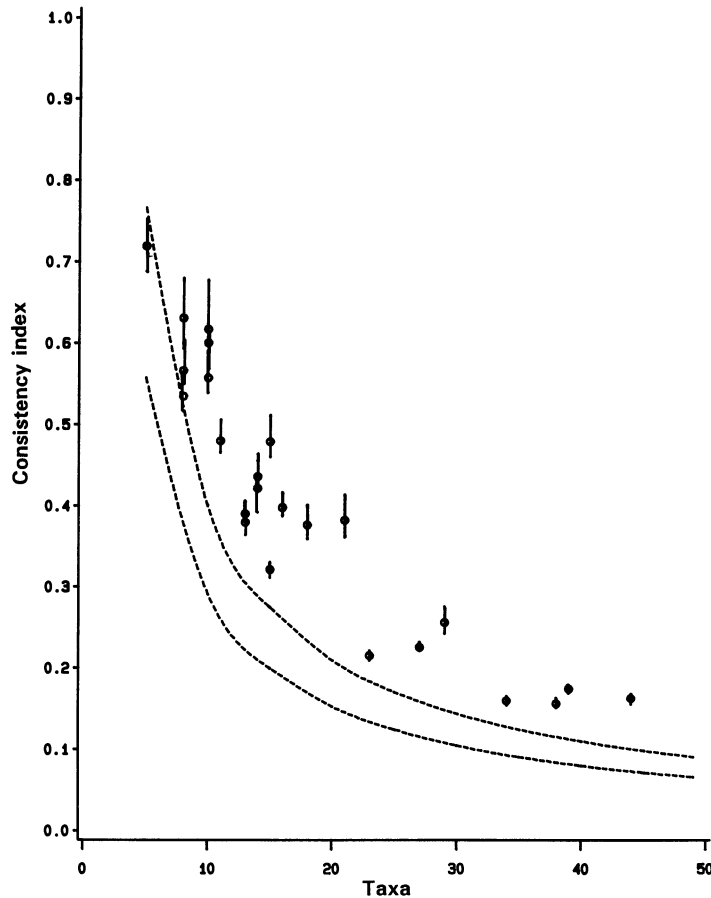


FIGURE 7. Comparison of Archie's (1989a) randomized CI values (ranges indicated by vertical bars) to 95% confidence limits (---) of CIs from our random data sets, for 5-49 taxa.

confidence limits of CI distribution for random data, indicating questionable support for topologies based on those real data. This is not to say that we believe any data sets exhibiting CIs greater than the marked confidence intervals are "good." The high random data CI values obtained for smaller data sets are a poignant reminder of the caution required when interpreting tree topologies. Additionally, this (and other) models of randomness are based only on independent character distributions and do not take into account suites of mutually congruent characters that are incongruent with the shortest tree (Farris, 1991).

A rescaling of the CI (CI_{adjusted}), taking the mean CI_{random} into account, might permit comparison among data sets. Simple

removal of random effects for a given number of taxa,

$$CI_{\text{adjusted}} = CI - CI_{\text{random}}, \quad (4)$$

appears to meet the criteria outlined by Archie (1989a, 1990) and Meier et al. (1991) for an adequate, comparative measure of homoplasy. CI_{adjusted} is not correlated with number of taxa (Fig. 8), and the absence of phylogenetic information is represented by a value of zero.

Despite meeting these criteria, we have reservations regarding the use of CI_{adjusted} for comparison among data sets. Because the internal structure of a data set can immensely influence the range of possible tree lengths and CIs, homoplasy measures that do not take character-state frequencies

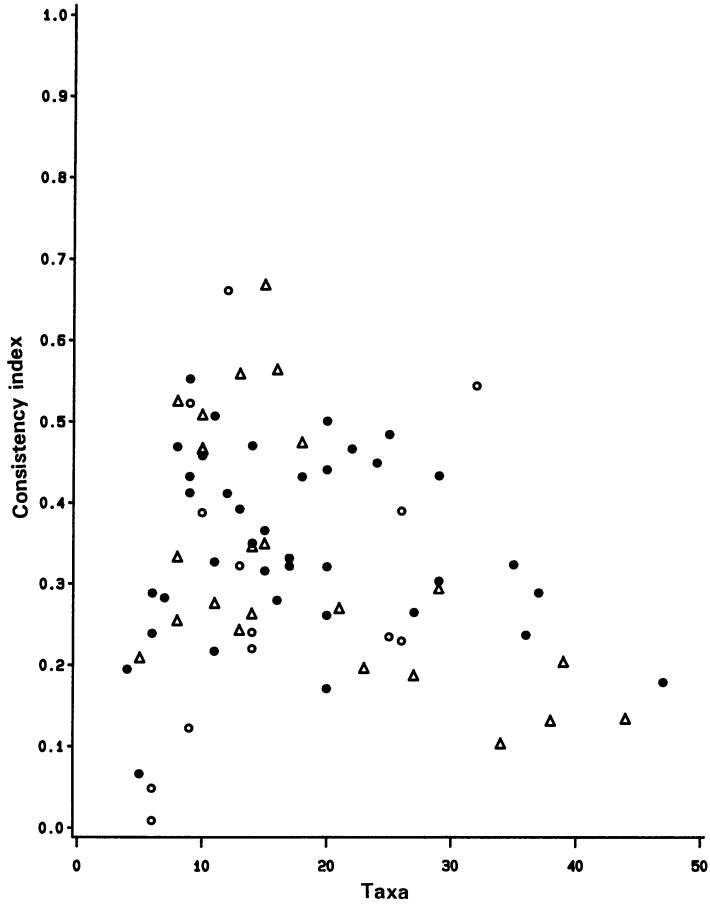


FIGURE 8. Adjusted CI values for CIs from published literature. Δ , Archie (1989a); \circ , Sanderson and Donoghue (1989, molecular data); \bullet , Sanderson and Donoghue (1989, morphological data).

into account can only be used to compare data sets under very limited conditions. Ideally, each individual character of a data set should have a matching character-state frequency in the compared data set. At the very least, data sets should exhibit plesiomorphic to apomorphic character-state ratios that are equal to one another. Even this latter, less stringent condition is unlikely to be met in most instances. There is currently no homoplasy measure that is sensitive to data set structure and is simultaneously uncorrelated with number of taxa. We are in agreement with Meier et al. (1991:84), who suggested "exercising caution when comparing data sets of radically different internal structure."

Direct comparison of homoplasy levels among data sets remains problematic, even with the availability of homoplasy indices that are free of the effect of number of taxa and characters (HSR and $CI_{adjusted}$). Without a reliable comparative statistic, the best alternative is to judge a data set on its variance from a random result. With Equation 4, above, we provide a crude method for testing randomness by comparing actual CIs with random CIs, but we recognize its limitations due to its insensitivity to internal structure of a data set. Archie's (1989a, 1989b) randomization procedure and that of Faith and Cranston (1991) are specifically designed to deal with character-state frequencies. In our view, Archie's

or similar methods hold the most promise for evaluating a given data set and its variance from random. However, as pointed out by Faith and Cranston (1991) and Farris (1991), rejecting the null hypothesis of random permutation does not necessarily provide confidence in phylogenetic conclusions.

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